

ZYGEUPOLIA LITORALIS, A NEW HETERONEMERTEAN.¹

BY CAROLINE BURLING THOMPSON, PH.D.

I. INTRODUCTION.

1. Methods.
2. Habitat.
3. The living worm.

II. ANATOMY.

1. Body wall.
 - a. Epithelium.
 - b. Cutis.
 - c. Musculature.
2. Nervous system.
3. Sense organs.
 - a. Cerebral organs.
 - b. Lateral grooves.
4. Rhynchodæum.
5. Rhynchocoel and proboscis sheath.
6. Proboscis.
7. Blood vascular system.
8. Excretory system.
9. Alimentary system.
10. Reproductive system.
11. The caudicle.

III. PARASITES.

IV. GENERAL CONCLUSIONS.

V. LITERATURE LIST.

VI. EXPLANATION OF PLATES.

PLATES XL-XLIV.

I. INTRODUCTION.

At the end of August, 1899, four specimens of *Zygeupolia litoralis* were discovered by the writer at Wood's Hole, Mass. The following summer the worms were found in great abundance in the same locality, and from fifty to one hundred specimens were obtained.

The work on this paper has been mostly done in the Zoological Laboratory of the University of Pennsylvania, under the direction of Prof. E. G. Conklin and Asst. Prof. T. H. Montgomery, Jr., and it is a pleasure to express my thanks to both for their interest

¹ Contribution from the Zoological Laboratory of the University of Pennsylvania.

and generous assistance. To Dr. Montgomery, who has more directly supervised my work and kindly helped me in many ways, I am especially grateful. I would also thank Dr. C. O. Whitman for the courtesies extended me at the Marine Biological Laboratory at Wood's Hole, and I am indebted to Dr. Wesley R. Coe for many kindnesses.

METHODS.—Owing to the great contractility of the Nemerteans, it is best to use some stupefying agent before fixation, otherwise the specimen becomes so twisted that it is unfavorable for sectioning. After removing the slime sheaths with a needle, the worms were usually placed in a shallow dish of sea-water, and crystals of magnesium sulphate were slowly added. If dropped in too quickly they will irritate the worms and fragmentation will occur. In this solution the worms were left until they ceased to respond when touched, the time varying from one and a half to three hours, according to the amount of the sulphate. When the worms were sufficiently relaxed the water was drawn off, and the killing fluid added; or they were lifted out of the water with brushes and placed in the fixative.

The fixatives used are (1) corrosive sublimate, a concentrated solution in fifty per cent. alcohol, for thirty minutes; an excellent general fixative, and one that has been extensively used in this work. (2) Gilson's mercurio-nitric mixture, formula according to Lee (1896), for about half an hour; to be highly recommended, especially for the structure of gland cells and connective tissue. (3) Flemming's fluid (chromo-aceto-osmic acid), for twenty-four to sixty hours; especially good for nerve tissue and cilia. (4) Flemming's fluid (stronger mixture), for forty-eight hours, followed by pyroligneous acid for twenty-four hours. After employing this method the material may be sectioned and mounted without staining. It is excellent for tracing nerves, and for the gross anatomy of most parts, but it is not adapted for histological or cytological details, except for cilia. Specimens fixed in this way may afterward be stained with iron-haematoxylin, but the results are not so good as when Flemming's fluid alone is used. (5) Ninety-five per cent. alcohol; a good fixative, except for the body epithelium.

The stains used are Ehrlich's haematoxylin, undiluted, fifteen minutes to one hour, washed with alcohol containing a few drops

of ammonia and followed by eosin in concentrated aqueous solution, three to five minutes. This is the stain that has been most used, and is a very satisfactory one. The longer time in hæmatoxylin is best for nerve fibrous tissue and epithelial structures. The Biondi-Ehrlich mixture, three hours, has been employed, but is not very satisfactory except for connective tissue. The iron-hæmatoxylin method together with Bordeaux red is an excellent stain after a Flemming fixation, and the Hermann triple stain—saffronin twenty-four hours, gentian violet six minutes, iodine three hours—has also been used.

HABITAT.—*Zygeupolia* was found at Wood's Hole, in a sandy beach of limited extent, bordering on a little arm of Buzzard's Bay that is separated from the main bay by the point of land known as Penzance. Here, just in the angle made by the bay shore and Penzance, the sand has drifted in, replacing the usual stony or pebbly beach; and in this small area, which is uncovered at low tide, are found, together with many other marine worms, especially Annelids, several genera and species of Nemerteans. Both *Cerebratulus leidy* Verr. and *C. lacteus* Verr. occur there, but the latter not abundantly; *Micrura caeca* Verr., *Cephalothrix linearis* Oers. and *Carinoma tremaphoros* Thomp. With such a rich supply of material in a spot very convenient to the Marine Biological Laboratory, it seemed unprofitable at that time to work over any other localities, so I am unable to say anything in regard to the distribution of *Zygeupolia*. Dr. Coe found this genus last summer in Quisset Harbor, about two miles farther north on Buzzard's Bay, in a very similar habitat.

When the sand, either above or below the low-water mark, is turned over, *Zygeupolia* may be found, usually about a foot below the surface. The turning up of the sand frequently breaks the worm, but a number of perfect specimens have been preserved.

THE LIVING WORM.—In life the worms vary considerably in length, chiefly owing to different states of contraction, so that it is difficult to say accurately what the true length is. The same worm seems to have two normal states, beside that of actual contraction. The first is that of comparative rest, seen in Pl. XL, figs. 5, 6, which are sketches from living worms. In this condition, as when lying undisturbed in a dish of water, the average length is from 6–8 cm. But when in motion, crawling along the sides of the dish, the worm becomes greatly extended, so that the indi-

vidual that in rest measured 6-8 cm. may now be 10-12 cm. or longer.

A change in color accompanies the elongation. At rest the body has a decidedly pink color; in extension the body is more transparent and dull brownish. This may be seen by comparing the extended worm in fig. 4 with figs. 5 and 6. As the pink color is most pronounced in the contracted condition, becomes less so at rest and disappears in extension, it is probably due to muscular contraction. The width varies in different specimens from $1\frac{1}{2}$ -3 mm.; it also varies in the same specimen according to the state of contraction.

In the living worm, Pl. XL, figs. 4, 5, 6, four different regions may be distinguished: (1) the head, (2) the anterior part of the body, (3) the posterior part of the body, and (4) the caudicle.

The head is about 6 mm. long, not separated from the body, pure white and tapering to a very fine point. There are no lateral slits, the ciliated pits of the cerebral organs opening directly to the exterior. The mouth is a very small round opening on the ventral surface. The shape and color of the head, together with the absence of lateral slits, are good criteria for determining the genus.

The anterior part of the body is the region extending from the mouth to the beginning of the lobed middle intestine. The length is from $1\frac{1}{2}$ - $3\frac{1}{2}$ cm., and the color varies from pale yellow to pinkish. It is rounded and more or less swollen, owing to the presence there of the greater part of the proboscis.

The posterior part of the body is the most extensive. It is somewhat flattened in life but is always rounded in preserved specimens. The color varies from rose color to pale yellow, light brown and chocolate brown. A pinkish median line on the dorsal surface represents the rhynchocoel; the alternating cross lines of light and dark on each side of the median line, fig. 5, are the gonads and intestinal caeca respectively.

A series of observations were made to ascertain if there are any appreciable color variations corresponding with sexual maturity or difference of sex. The conclusions reached are (1) that there is no difference in the color of sexually mature and immature individuals, except that the increased size of the gonads in the mature specimen causes the cross lines mentioned above to be more pronounced; (2) that the general color of the body is the same for

males and females; (3) that the color of the intestinal caeca is dependent upon the amount and character of the food contents. The intestine in freshly taken worms is much darker in color than in specimens that have been kept in an aquarium for several days without food.

The caudicle in life appears as a slender white thread at the posterior end of the body, figs. 4, 5, 6. It is usually much twisted and is easily broken off. It should be mentioned here that in none of the four specimens that were first obtained in 1899 was the caudicle preserved, so that the presence of this appendage is not mentioned in my preliminary note, Thompson (1900 *a*).

The white spots in the posterior part of the worm, slightly exaggerated in fig. 6, are parasites and will be described under that heading.

On account of its transparency the living worm is a most favorable and interesting object for study with the low powers of the microscope. It should first be slightly stupefied to prevent excessive movements and contractions, so that when it is placed on the slide with a few drops of sea-water and covered, the muscles relax and it lies quietly there, fully extended. With a magnification of about 70 diameters, it is possible to study the brain lobes and commissures, the cerebral organs, the blood vessels of the head, the proboscis and rhynchodaum, the alimentary system and the gonads. In only two cases could the nephridia be distinguished, but nothing was determined as to their structure. Several attempts were made to study the worm by treatment with methylen blue, after the method of Bürger (1891, p. 327, footnote), but without success.

The results obtained from the study of the organs in life will be incorporated in the several sections relating to the different organ systems.

II. ANATOMY.

BODY WALL. — *a. Body Epithelium.* — The body epithelium, fig. 2, is a high one-celled layer, consisting of ciliated supporting cells, *S.C.*, and gland cells, *Gl.*₁, *Gl.*₂, resting upon a basement layer, *B.L.* Interstitial connective tissue cells are always present in varying numbers between the bases of the epithelial elements.

The supporting cells, fig. 14, are about .035 mm. in height,

broad at the free distal ends where the cilia are borne, and tapering proximally to a slender stalk, *st.*, which constitutes about two-thirds of the length. In fig. 15, drawn from a sublimate preparation, the stalk is somewhat shrunken and appears less than half the length of the expanded distal part; in fig. 14, a Flemming's fluid preparation, the stalks are relatively longer, and probably more as they appear in life. The oval nucleus, *N.*, lies in the tapering part of the cell, just above the stalk. The chromatin forms a prominent reticulum.

The cilia, *Cl.*, are about as long as the expanded distal part of the cell. Each cilium is composed of several parts. The basal knob, fig. 14, *b.k.*, rests on the distal surface of the cell, and is connected by a fine thread with a second smaller granule, the upper knob, *u.k.*, which bears the terminal hair of the cilium. The cilium is continued into the cytoplasm by a line of very fine granules, fig. 14, *x.*, which seem to reach the nucleus. This, however, can only be seen with a very high magnification.

The gland cells are abundant in the body epithelium, and are uniformly distributed throughout the body. Two types may be distinguished, in the first the secretion stains with eosin, fig. 2, *GL.*₁, in the second with hæmatoxylin, fig. 2, *GL.*₂. In both types a delicate cell membrane is present, the nucleus is small and lies at the base of the cell embedded in cytoplasm. The relative amounts of cytoplasm and secretion depend upon the phase of the cell. In fig. 2 the blue-staining cell on the left contains less secretion and more cytoplasm, and is therefore in an earlier phase than the blue-staining cell to the right. In like manner, the red-staining cell on the right of the figure contains less secretion and is in an earlier stage than the red-staining cell on the left. The red-staining secretion is homogeneous, evidently fluid or viscous; the blue-staining secretion apparently contains flaky masses within a fluid. The latter cells are more apt to assume the flask-like shape, the former are oftener rod-shaped. Cells are frequently found with the secretion entirely discharged from the delicate cell membrane, the nucleus remaining at the base.

The basement layer, fig. 2, *B.L.*, separates the epithelial cells from the underlying musculature. It is not a true basement membrane, being not the product of the bases of the epithelial cells, but a formation from the interlacing fibres of connective tissue

cells. The nuclei of the component connective tissue cells are seen with difficulty, but occur here and there embedded in the fibres. With a low power the basement layer has a homogeneous, rather gelatinous appearance, but with higher magnification its true fibrous structure is seen. The average height of the basement layer in the head region is about .006 mm., but it is not a layer of uniform thickness, for its outer surface is thrown into a series of small elevations and depressions. The ridges on the surface bear the stalks of the supporting cells, while the gland cells are inserted into the pits or depressions. The basement layer does not stain with hæmatoxylin-eosin, but takes a faint pink with the Biondi-Ehrlich stain.

An epithelial musculature of circular muscle fibres, fig. 2, *Ep.m.*, is present immediately beneath the basement layer. It is especially well developed in the head region, consisting of a number of fibres like those of the body wall. Posterior to the œsophageal region the epithelial muscle layer becomes very thin and finally disappears, but reappears at the posterior end of the body.

b. The Cutis.—The cutis is defined by Bürger (1895) as the subepithelial glandular layer, usually containing numerous muscle fibres, which is found in the Heteronemerteans.

In *Zygeupolia* any distinction between the outer longitudinal muscle layer and the cutis would be merely an artificial one. The fibres of the outer longitudinal muscle layer extend from the circular layer out to the epithelium of the body wall, and although subepithelial gland cells are present, frequently in great numbers, they are not restricted to the peripheral portion of the layer, but often extend in as far as the circular muscle. It is thus evident that in *Zygeupolia* the term cutis is synonymous with outer longitudinal muscle layer. In this respect *Zygeupolia* differs greatly from the genus *Eupolia*, in which a cutis distinct from the outer longitudinal muscle layer is present.

The finer structure of the cutis, or of the outer longitudinal muscle layer, may be seen in fig. 2. Each longitudinal muscle fibre, *L.M.f.*, is surrounded by a sheath of connective tissue, composed of the slender processes of the connective tissue cells which are present between the muscle fibres. These cells are greatly branched, their nuclei, *Cn.T.N.*, are oval, and contain a small amount of chromatin. Slender radial muscle fibres, *r.m.f.*, trav-

erse the cutis, and here and there detached circularly running fibres, *M.s.*, occur.

The subepithelial gland cells, or, as Bürger terms them, the cutis gland cells, are present throughout the body in the outer longitudinal muscle layer. Two, and possibly three, types of glands may be distinguished.

The first type is a multinucleate structure, fig. 2, *Cu. Gl.*₂, staining with hæmatoxylin. Such a gland is the probable result of the fusion, phylogenetically, of several simple cells. The proximal portion resembles a bunch of grapes, each grape representing a cell with its nucleus; the distal part is a long, slender duct, opening to the exterior between the epidermal cells. The length of the blue-staining cells varies in different parts of the body. In the head region, fig. 2, they are very long, extending in from the epithelium nearly to the rhynchodæum. In the posterior part of the body, fig. 15, *Cu. Gl.*₂, their length has diminished more than one-half.

The second type is a cell, staining red with eosin, having the shape of a very slender flask with a long neck, figs. 2, 15, *Cu. Gl.*₁. Only one nucleus is present, at the basal end of the cell, and a delicate cell membrane may be distinguished.

Two quite distinct appearances have been observed in the red-staining cells. These may be morphologically different cells, or merely phases of the one type. In the one, figs. 2, 15, *Cu. Gl.*₁, the granules are very fine, close together, and stain a rose red; in the other, fig. 15, *Cu. Gl.*_{1b}, the granules are large, rounded and a brighter, more metallic red. The facts that no transition stages have been observed, and that the two varieties have a slightly different distribution, may indicate that they are morphologically different.

The distribution of the cutis gland cells is a point of some interest and, so far as I am aware, has not been worked out in any detail among the other Nemerteans. In certain parts of the body the gland cells are aggregated into very prominent zones, and it seems probable that these glandular areas have some important physiological function, which is as yet undetermined, aside from the usual one of producing the slime sheath for the body.

Diagram 1 illustrates the distribution of the cutis gland cells.

It is seen here that the most anterior part of the head is entirely free from cutis gland cells, but that about 0.5 mm. behind the tip the blue-staining cells are very abundant, distributed uniformly on all surfaces of the body. The red-staining cells occur in small numbers and are mostly on the ventral surface; they are of the finely granular variety. From the mouth back to some distance behind the nephridia the blue-staining cells are quite numerous, interspersed with the red-staining cells. Just behind the great rhynchocoelomic expansion, where the circular muscle of the body wall is considerably thickened, comes a region that might properly be called a *glandular zone*, *Gl.Z.*, owing to the enormous increase in the number of the cutis gland cells. The whole outer longitudinal muscle layer is so crowded with them that in a cross section the muscle fibres seem nearly obliterated. The cells increase also in size, or perhaps are more distended with secretion. The blue-staining cells are more abundant than the red. This zone extends backward for about 3 mm., then suddenly ends, just in front of the two lateral grooves, *L. G.*

In the lateral groove region, fig. 23, *Cu. Gl.*₁, *Cu. Gl.*₂, the blue cells are confined to two tracts, one on each side of the body, above the lateral nerves. The red-staining cells are in four tracts, dorsal

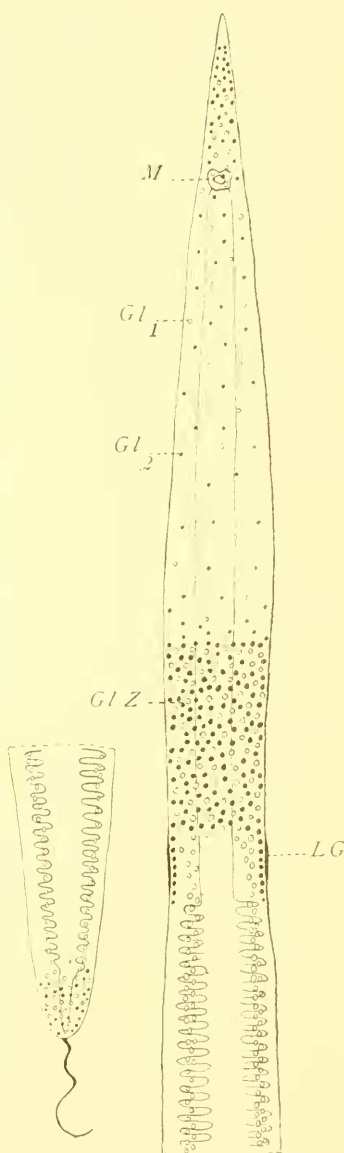


Diagram 1.—The head and part of the body of *Zygeupolia*, illustrating the distribution of the cutis gland cells.—The outline of the alimentary tract is given as a means of orientation. *Gl.*₁, red-staining cutis gland cell; *Gl.*₂, blue-staining cutis gland cell; *Gl.Z.*, glandular zone; *L. G.*, lateral groove; *M.*, mouth.

and ventral to the blue tracts. The red-staining cells in this region and in the preceding *glandular zone* are of the coarse granular variety.

After the beginning of the middle intestine and its pouches, the blue-staining cells are no longer present, except at the most posterior end of the body. The four tracts of red-staining cells, however, continue along the entire length of the intestine. Owing to the increased size of the intestinal cæca and the gonads, the body wall is stretched and the muscular layers are thin, so that the red gland cells can reach down only a short distance, and are consequently short, often appearing more like epithelial cells.

At the extreme posterior end of the body both red and blue cells are present in great numbers all around the body. The red cells are the more abundant, and are considerably larger than the blue (see fig. 15). Both fine and coarse varieties occur.

There is no cutis in the caudicle, so that cutis gland cells are necessarily absent.

c. The Body Musculature.—The entire region of the head in front of the brain, Plate XLI, fig. 18, from the epithelium, *Ep.*, in to the rhynchodæum, *Rd.*, is made up of longitudinal muscle fibres, *L.M.*, with interlacing radial muscle fibres, *r.m.f.* Except for the cerebral nerves, *C.N.*, and the cutis gland cells, *Cu.Gl.*, and probably some very fine blood lacunæ, no other organs are present. The wall of the rhynchodæum, which will be described under that heading, contains four stout bundles of longitudinal muscle, *Rd.M.*

Just anterior to the attachment of the proboscis to the body wall, the inner ends of the radial fibres interlace more closely about the rhynchodæum, until a ring of circular muscle, fig. 18, *C.M.*, is formed, which becomes the circular muscle of the proboscis sheath. Behind the attachment of the proboscis, fig. 19, *y.*, the outermost circular fibres separate off from the rest, thus forming the circular muscle of the body wall, fig. 19, *C.M.*, outside the proboscis sheath. The longitudinal fibres lying between, fig. 20, *i.L.M.*, represent the beginning of the inner longitudinal muscle.

Both dorsal and ventral brain lobes, fig. 19, *D.L.* and *V.L.*, lie outside the circular muscle, *C.M.*, in the outer longitudinal layer; but the cerebral organs, fig. 21, *C.Org.*, which are directly behind the dorsal lobes and receive their nerve supply from them, lie within

the circular muscle, in the inner longitudinal layer. At the posterior end of the dorsal lobes the following changes may be noted. The circular fibres, figs. 19, 20, *C.M.*, at first all run along the inner surface of the end of the dorsal ganglion and beginning of the cerebral organ, then a few fibres bend out and curve around the sense organ on its outer side, until finally all the muscle fibres lie on the outside of the cerebral organ, fig. 21, *C.M.* The ventral ganglia lie as before, outside the circular muscle.

Just in front of the mouth a strong band of muscle, fig. 21, *H.M.*, runs from side to side, beneath the rhynchocœl and above the median blood vessel.

In the œsophageal region, fig. 22, there is nothing unusual in the structure of the muscle layers; the outer longitudinal, *o.L.M.*, is the thickest, and next the circular, *C.M.* This arrangement continues past the nephridia into the region of the expanded rhynchocœl, where all layers of the body wall are greatly stretched, and consequently very thin.

A short distance anterior to the middle intestine the rhynchocœlomic dilation ceases and the diameter of the rhynchocœl is about equal to that of the œsophageal region, while its walls are frequently folded and constricted. In this part of the body the circular muscle of the body wall becomes greatly thickened (see Plate XLIV, fig. 62, *C.M.*).

Inner Circular Muscle.—Fig. 23, Plate XLI, is a cross section of the body just anterior to the beginning of the middle intestine. The diameter of the body is less than in the œsophageal region (cf. fig. 22), and much less than in the great expanded portion which is not figured. The outer longitudinal muscle in fig. 23 needs no description; the circular muscle is relatively thicker than in the anterior part of the body, but not greatly enlarged. The circular muscle of the proboscis sheath has increased greatly in size and some of its outer fibres run ventrally, making a band of circular muscle, *i.C.M.*, that encircles the stomach, *S.* Other fibres, apparently from the circular muscle of the body wall, join with these, running dorso-ventrally, and crossing the inner longitudinal layer dorsally and ventrally. In short, *an inner circular muscle layer is here present; and muscular crosses occur between it and the outer circular layer, both dorsally and ventrally* (see fig. 23, *D.m.cr.*, *V.m.cr.*). A few sections posterior to the one

figured in fig. 23, the inner circular muscle layer suddenly ends and the first pair of cæca of the middle intestine appear. On examining the sections anterior to fig. 23, it is found that the inner circular muscle extends forward for about 1.8 mm. as a very thin layer of a few fibres (see Plate XLII, fig. 30, *i.C.M.*), the thickened region, as in fig. 23, only extending over a few sections.

At its beginning the inner circular muscle, as seen in cross sections, measures about .006 mm. dorso-ventrally; over the greater part of its extent the measurements range from .012–.017 mm.; then suddenly increase from .023 to .06 in about five sections of 6μ each; finally just before the end, fig. 23, the layer is .087 mm. thick.

The inner circular muscle encloses a band of longitudinal muscle fibres on the dorsal side of the stomach, below the rhynchocoel, Plate XLII, figs. 23, 30, *i.L.M.*

The fibres of the inner circular muscle layer are direct continuations of fibres from the circular layer of the proboscis sheath. Furthermore, in the anterior part of the layer, the fibres come from the inner surface of the proboscis sheath, bend out, cross the outer fibres and then continue down around the stomach. This bending out and crossing is shown in fig. 30, *z*. In a more posterior position, the inner circular layer becomes thicker and consists of fibres from the outermost part of the proboscis sheath, together with fibres from the circular muscle of the body wall. It is thus seen that the partial origin of the inner circular muscle layer of *Zygeupolia* from the proboscis sheath circular muscle is beyond a doubt.

An inner circular muscle layer has not been heretofore described, as such, for any Heteronemertean. I have found a very similar layer in *Micrura cæca*, with a considerable thickening at the posterior end, but this has not been mentioned in any published work, so far as I am aware. Coe (1901) describes in *Micrura alaskensis* a structure that might properly be called an inner circular muscle layer. He says, p. 72: "The delicate layer of circular and longitudinal muscular fibers which surrounds the epithelial lining of the esophagus in most of the Heteronemerteans becomes remarkably developed in this species. At the very posterior end of the esophagus—just anterior to the

first intestinal pouches—the circular muscles of the esophagus increase so greatly in number that they form a most conspicuous layer. In the region of its maximum development this layer becomes nearly half as thick as the circular layer of the body walls in the same section. In no other species of the Lineidae has this muscle been found of even approximately this thickness. Its fibers connect in part with the circular layer of the body walls and to a lesser degree with the circular muscles of the proboscis sheath. But few fibers lie on the dorsal wall of the esophagus, so that this organ is largely bound up with the proboscis sheath in a continuous layer of muscles, and one cannot fail to see the striking resemblance between this circular layer and the inner circular muscles that are so highly developed in precisely the same region in *Carinoma*."

Since, as Dr. Coe says, the resemblance between this muscular layer and the inner circular layer of *Carinoma* is so striking, why should we not regard them as one and the same structure, that is, as homologous? In what particulars do they differ?

Bürger (1895), p. 234, gives the following definition for the inner circular muscle layer of the Protonemertean and *Carinoma*. "Die Leibesmusculatur. Zu dieser rechne ich einen aus Ringfibrillen zusammengesetzten Muskelschlauch, welcher bei den Protonemertinen, vor allem bei *Carinina grata* und *Carinella polymorpha*, *superba* und *linearis*, und unter den Mesonemertinen bei *Carinoma armandi* um Vorderdarm und Rhynchocölon entwickelt ist, diese beiden Hohleylinder einschliessend. Diesen Muskelschlauch nenne ich die innere Ringmuskelschicht." Bürger also states that the fibres of the inner circular muscle differ in no way from those of the body wall.

Bürger further speaks, p. 235, of the crossing of fibres that frequently occurs in the dorsal and ventral median line of the body, between the inner circular and the outer circular layer of the body wall. "Eine sehr merkwürdige Erscheinung wird dadurch hervorgerufen, dass die innere Ringmuskelschicht in Beziehung zur äusseren Ringmuskelschicht, also der Ringmuskelschicht des Hautmuskelschlauchs tritt. Das geschieht, indem dorsal und ventral in der Medianebene des Thierkörpers von links und rechts Muskelfasern aus dem Verbande beider Ringmuskelschichten heraustreten, und, die Längsmuskelschicht des Haut-

muskelschlauchs durchdringend, die von der einen Ringmuskelschicht kommenden über Kreuz an die andere hinantreten."

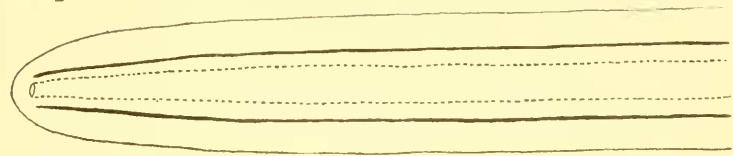
The definition, then, of the inner circular muscle is a layer of circular muscle fibres that encloses the rhynchocoel and anterior intestine, the individual fibres being just like those of the body wall.

Since there is a common agreement with Bürger's definition among the three muscle layers under discussion, namely, that in *Micrura alaskensis*, that in *Zygeupolia*, fig. 23, *i. C. M.*, and that in *Micrura caeca*; and furthermore, since all three layers have muscular crosses between themselves and the circular muscle of the body wall, I can see no reason why each should not with all propriety be termed an inner circular muscle layer, homologous with that of the Proto- and Mesonemerteans.

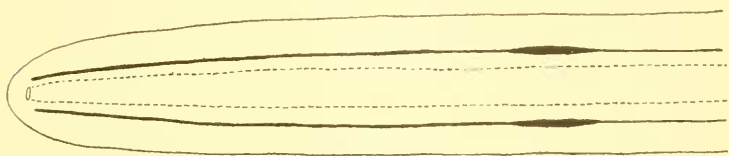
The only difference between the inner circular muscle layer of *Zygeupolia* and that of the Carinellas and *Carinoma* is in the amount of surrounding connective tissue, the body "parenchym" of Bürger. In *Zygeupolia* this tissue is present only around the blood vessels, so that the inner circular muscle layer adjoins the inner longitudinal muscle layer, except where the blood vessels intervene. In this particular *Zygeupolia* resembles *Carinina*, for in *Carinina* the inner circular muscle borders directly on the longitudinal muscle, and there is no intervening layer of "Leibesparenchym."

The presence of the inner circular muscle layer and the muscular crosses in *Zygeupolia* and *Micrura* is important when viewed from a phylogenetic standpoint. This peculiar region of the body, just in front of the middle intestine, is by far the most interesting part of the whole trunk, for it has unaccountably remained in a primitive condition, as comparison with other Nemerteans will show.

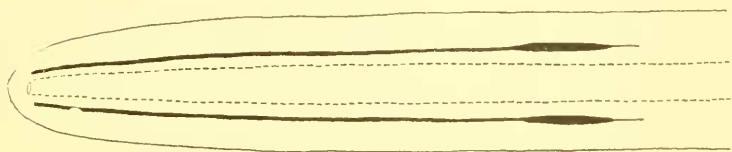
Diagram 2 is a representation of the stages, illustrated by living, more primitive genera, through which the inner circular muscle of *Zygeupolia* and *Micrura* may have passed. A, represents the most primitive condition, found in *Carinella annulata*, in which the inner circular muscle is a thin layer of uniform thickness, extending throughout the body; in B, *Carinella polymorpha*, the muscle is co-extensive with the body, but is thickened in a certain region; in C, *Carinella linearis*, the muscle ends shortly behind the thickened region; in D, *Carinoma*, the muscle ends



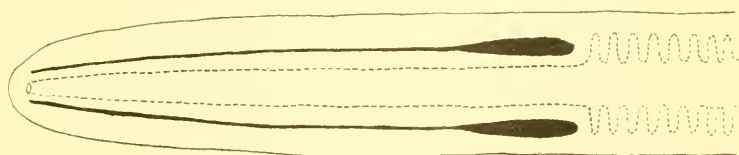
A



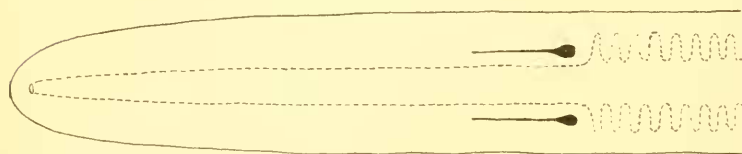
B



C



D



E

Diagram 2.—Showing the comparative extent of the inner circular muscle layer in certain Nemerteans.—A, *Carinella annulata*; B, *Carinella polymorpha*; C, *Carinella linearis*; D, *Carinoma*; E, *Zygeupolia* and *Micrura caeca*. The heavy lines represent the extent of the inner circular muscle, the broken lines the outline of the alimentary tract.

with an enormous thickening just in front of the middle intestine; E, shows the condition in *Zygeupolia* and *Micrura*. In the last two forms the inner circular layer is absent from the entire oesophageal region, and is represented merely by the thickened part in front of the middle intestine, and a short, thin, anterior extension of this.²

In this connection it is interesting to note that in *Cephalothrix aliena*, a new species from the Maldive Islands recently described by Punnett (1901 a), a very delicate inner circular muscle layer is present in the oesophageal region.

From the facts just enumerated it is evident that the inner circular muscle of the Heteronemertean may be regarded as the remnant of a layer once continuous throughout the body.

The accompanying table shows the comparative extent of the inner circular muscle layer in the different genera in which it occurs.

The second part, relating to the muscular crosses between inner and outer circular layers, shows that there is great variation in this respect in the genus *Carinella*.

² The facts in regard to the distribution and structure of the inner circular muscle in the genus *Carinella* have been obtained from Bürger's monograph.

	Inner Circular Muscle.		Crosses between Inner Circ. Muscle and Outer Circ. Muscle.	Position of Crosses.
	Structure.	Extent.		
<i>Carinina grata</i> ,	thicker in nephridial region	throughout body (?)	ventral cross only	in region posterior to nephridia
<i>Carinella</i> — a. <i>superba</i> ,	uniform thickness	throughout body	dorsal and ventral	throughout body
b. <i>annulata</i> ,	uniform thickness	throughout body	dorsal only	throughout body
<i>Carinella banyulensis</i> ,	thinner in nephridial region	throughout body	dorsal cross only	in nephridial region
<i>Carinella rubicunda</i> ,	thinner posterior to nephridial region	throughout body	wanting	
<i>Carinella polymorpha</i> ,	thicker in nephridial region, very thin posterior to nephridia	throughout body	dorsal cross faint, ventral cross wanting	throughout body
<i>Carinella linearis</i> ,	thicker in nephridial region, thin posterior to nephridia	from the mouth to nephridia, and a short distance behind them	wanting	
<i>Callinera bürgeri</i> Berg.,	thinner behind "rhynchoeol muscle sack"	from the mouth to close behind the "rhynchoeol muscle sack"	wanting	
<i>Hubrechtia</i> ,	uniformly thin	throughout body (?)	wanting	
<i>Carinoma</i> ,	great thickening at nephridia	from mouth to end of nephridial region	dorsal and ventral	from the mouth to end of nephridial region
<i>Cephalothrix atina</i> Punnett,	very thin, delicate layer	oesophageal region only	(?)	
<i>Zygucupolia</i> ,	absent in oesophageal region, appears as a thin layer about 2 mm. anterior to middle intestine, very thick at posterior end	extends forward for 2 mm. just anterior to middle intestine	dorsal and ventral	at posterior end of the inner circular muscle
<i>Micrura</i> ,	absent in oesophageal region, appears as a thin layer a short distance in front of the middle intestine, quite thick at posterior end	extends forward a short distance in front of middle intestine	dorsal and ventral	at posterior end of the inner circular muscle

The question now arises, can the so-called "oesophageal muscle" (Darmmuscultur, Bürger) be correlated in any way with the inner circular muscle?

Bürger (1895), p. 257, speaks of a musculature ("Darmmusculation") that is developed in the Meso-, Meta- and Heteronemerteans around the posterior part of the oesophagus, consisting of both longitudinal and circular fibres, the fibres being more slender than those of the body wall.

On p. 237 the same writer says that the dorso-ventral fibres that occur so frequently between the intestinal caeca, and also in the anterior part of the body, may be regarded as parts of a formerly continuous inner circular muscle layer. "Wir können die dorsoventrale Musculatur als eine innere Ringmuskelschicht, welche in lauter, in gewissen Abständen aufeinanderfolgende Ringe zerlegt wurde, vorstellen." He adds that sections of *Eupolia* and *Lineus geniculatus*, the latter figured on Taf. 20, Fig. 7, strengthen this opinion. In *L. geniculatus* the dorso-ventral fibres have bent around the intestine, on its dorsal as well as on its ventral face, making a continuous ring of circular muscle, and a crossing between these fibres and the circular muscle of the body wall takes place in the median ventral line.

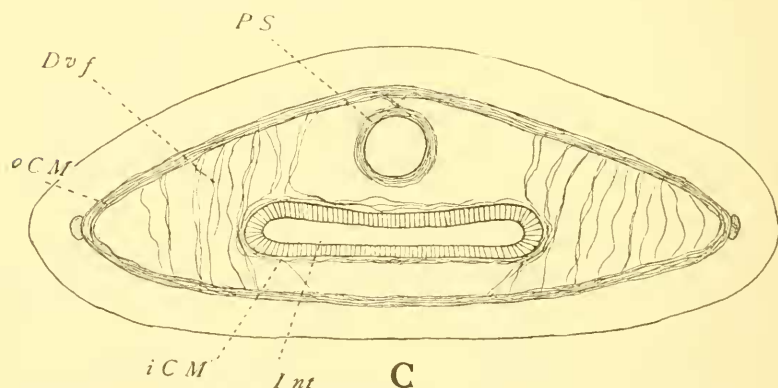


Diagram 3.—Cross section through the body of *Cerebratulus lacteus*, illustrating the deflection of the dorso-ventral muscle fibres into the inner circular muscle layer around the intestine.—*P.S.*, proboscis sheath; *o.C.M.*, outer circular muscle; *Int.*, intestine; *i.C.M.*, inner circular muscle; *D.v.f.*, dorso-ventral muscle fibres.

From my own observations upon *Cerebratulus lacteus*, *Lineus lacteus* and a *Lineus* sp., all preparations kindly lent by Dr. Montgomery, I find there is frequently quite a considerable layer of circular muscle fibres beneath the intestine, and also on its dorsal

side. These fibres may be almost invariably traced out of the circular sheath around the intestine into dorso-ventral fibres coming from the circular muscle of the body wall, or else into the circular muscle of the proboscis sheath. This is illustrated by Diagrams 3 and 4. The same is true in regard to the scattered fibres occa-

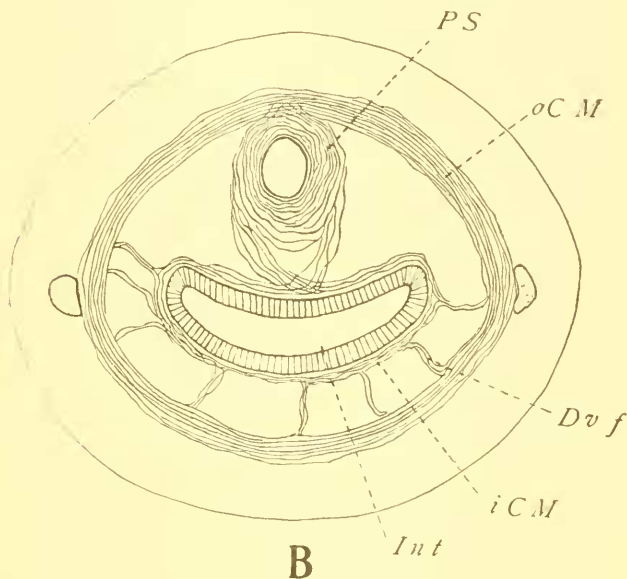


Diagram 4.—Cross section through the body of *Linus* sp.; illustrating the deflection of the dorso-ventral muscle fibres into the inner circular muscle layer around the intestine.—*P.S.*, proboscis sheath; *o.C.M.*, outer circular muscle; *Int.*, intestine; *i.C.M.*, inner circular muscle; *Dv.f.*, dorso-ventral muscle fibres.

sionally found above or below the œsophagus in *Zygeupolia*, which come from the body wall or the proboscis sheath, see Diagram 5.

It therefore seems that, if we accept the view of Bürger that the dorso-ventral fibres are derived from an original inner circular muscle layer, we may profitably go a step farther and say that the "Darmmuskulatur" or "œsophageal muscle," found around the dorsal as well as the ventral side of the œsophagus, is derived from the dorso-ventral fibres which have turned aside from their dorso-ventral course and have curved around the œsophagus so as to partially encircle it. If this is accepted we may then say that the "œsophageal muscle" is secondarily derived from the inner

circular muscle, two steps being involved in the phylogeny: first, the inner circular layer breaks up into detached groups of dorso-ventral fibres, then the latter turn out of their course and bend around the intestine to form the encircling "œsophageal muscle."

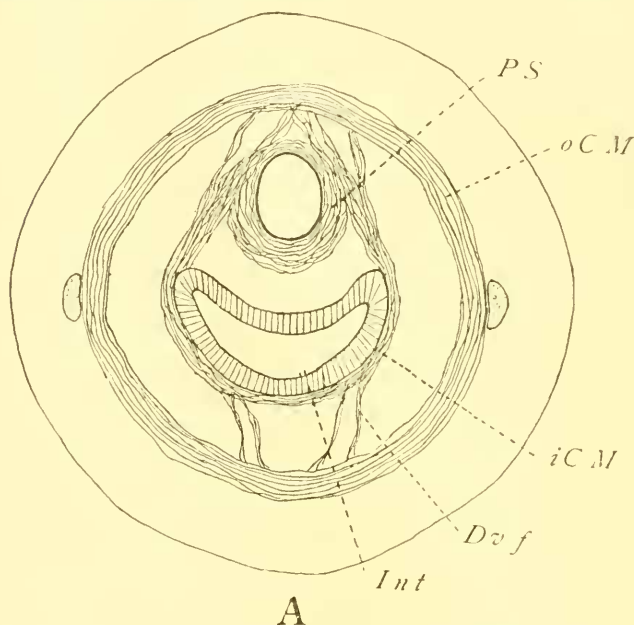


Diagram 5.—Cross section through the body of *Zygeupolia*, illustrating the deflection of the dorso-ventral muscle fibres into the inner circular muscle layer around the intestine —*P.S.*, proboscis sheath; *o.C.M.*, outer circular muscle; *Int.*, intestine; *i.C.M.*, inner circular muscle; *Dv.f.*, dorso-ventral muscle fibres.

This view is foreshadowed by Hubrecht (1887), p. 71, where he says: "I will not at present attempt to decide whether any of the muscular layers of the œsophagus, noticed both in *Eupolia* and *Cerebratulus*³ (Pl. VI, fig. 9, *a.m.*; Pl. XIII, fig. 6, *mt.*), may also be looked upon as derivatives of this inner circular layer . . . ;" and "Here, too [alluding to the *Schizonemertans*], I would be tempted to hazard a comparison between the absent inner circular layer and the musculature of the proboscis sheath."

To briefly summarize my views in regard to the presence and

³The *Cerebratulus* here alluded to is *C. corrugatus* = *Lineus corrugatus*, described by McIntosh (1879).

origin of the inner circular muscle layers in the Heteronemerteans: (1) the more or less delicate layer of circular muscle fibres encircling the alimentary tract in the œsophageal region of *Zygeupolia* and *Micrura* is a primitive structure, the remnant of a once extensive layer; (2) further investigation will probably demonstrate the presence of similar primitive remnants of an inner circular muscle layer in other Heteronemertean genera; (3) the "œsophageal muscle" fibres that frequently encircle the alimentary tract in the higher Lineidæ are continuations of deflected dorso-ventral muscle fibres. They are not primitive but of more recent structure, secondarily derived from the inner circular muscle layer by a breaking down of the latter into groups of dorso-ventral fibres.

The inner circular muscle layer ends with its great thickening just in front of the beginning of the middle intestine, so that posterior to this region the body musculature consists of the usual three layers—outer longitudinal, circular and inner longitudinal (see figs. 24, 25, 26)—which are very thin in the region of the gonads.

Histology of Muscular System.—Very little need be said in regard to the histology of the muscle. Each muscle fibre, as Bürger first demonstrated in 1890, is a single cell. The nuclei are long and stain deeply.

In Plate XL, fig. 13 is shown a portion of the circular muscle layer from the posterior end of the body, drawn from a section stained with iron-hæmatoxylin. At regular intervals, dark areas, *contr.*, are seen, alternating with light areas. The dark portions represent the most contracted part of the layer, the light a region of less contraction, or of rest. In the middle of the light areas, very faint indications may be seen of a smaller region of contraction. The contraction caused by fixation has evidently occurred in waves, as the regular intervals show. These contracted areas were first noticed in the Nemerteans by Hubrecht (1887).

Wagener (1863) describes "striated" muscle from a Nemer-tean, the genus of which is not mentioned. He says the striated areas ("Querstreifungen") alternate with thinner, lighter parts, and that the cross-stripping merges into a non-striated portion. A fibre separated from the bundle has a series of swellings ("Anschwellungen") on its surface. Wagener's Fig. 1, Taf.

IV, shows that what he regards as cross striations are evidently merely swollen, *i.e.*, contracted areas of the fibres.

2. THE NERVOUS SYSTEM.—*a. Anatomy.*—Bürger (1895) divides the nervous system of the Nemerteans into a central and a peripheral system. The former comprises the brain and lateral nerve chords, which have a thick investing layer of ganglion cells; the latter, all other nerves and nerve layers, provided with a thick ganglion cell envelope. Montgomery (1897 *b*), p. 382, includes in the central nervous system all parts provided with ganglion cells, namely: “(1) the dorsal and ventral brain lobes and commissures; (2) the lateral nerve chords . . . ; (3) the paired œsophageal nerves; (4) the longitudinal nerves of the proboscis . . . ; (5) the dorsal, unpaired, larger median nerve of the body wall; and probably also (6) the lesser, unpaired median nerve.”

The anatomy of the brain of *Zygeupolia* may be readily studied in life from a specimen compressed beneath a cover glass, for the head is so transparent that the parts are easily distinguished (see figs. 1, 16). The brain lies about 4 mm. behind the tip of the head, directly in front of the mouth, encircling the rhynchocœl, and consists of four lobes or ganglia of about equal size, two dorsal and two ventral. Viewed from the dorsal surface, the dorsal lobes, fig. 16, *D.L.*, are most prominent, and at their posterior ends are situated the pear-shaped cerebral organs, *C. Org.*, which are about one-third the length of the dorsal lobes and about one-half their width. The dorsal lobes are connected above the rhynchocœl by a slender commissure, which is very difficult to see in life, figs. 1, 16, *D.Comm.*, but is easily made out from sections. Its dorso-ventral measurements vary in different specimens from .04–.07 mm., probably owing to different states of contraction, or to the plane of the section. In the sections of one specimen, fig. 19, the dorsal commissure appeared to be composed of fibres coming from both dorsal and ventral lobes, an unusual condition, and one not previously described in Nemerteans, so far as I am aware. The ventral lobes are united by a stout commissure, about 14 mm. measured dorso-ventrally, that in life may be plainly seen, figs. 1, 16, shining through the rhynchocœl, which lies above it, and extending backward posterior to the dorsal commissure. Measured from side to side, both commissures are short, owing to the

close proximity of the brain lobes. The dorsal and ventral lobes of each side are connected anteriorly, as may be seen from sections, but the connection ends just posterior to the end of the ventral commissure, and from this point backward the dorsal and ventral lobes are quite separate. In life the ganglion cell layer appears distinct from the fibrous core of the brain and lateral chords, the former as a greenish-yellow investing layer, the latter as a clear silvery-gray central mass.

From sections it may be seen that both dorsal and ventral lobes are continued forward into the tip of the head as numerous slender nerves, which are approximately represented in Plate XL, fig. 1. No especial nerve endings have been observed. The dorsal lobes terminate as such just in front of the cerebral organs, and from their posterior ends arise the nerves that supply the cerebral organs. Immediately in front of the cerebral organ, the dorsal lobe gives off on its dorsal side a horn or prolongation of the fibrous core surrounded by ganglion cells. This horn ends shortly and is replaced posteriorly by the cerebral organ, but there is no connection between the two structures, for the cerebral organ derives its nervous matter from the ventral part of the dorsal lobe. The cerebral organ nerve enters the cerebral organ on the ventral side and afterward branches and ramifies, so that the nervous material is well distributed throughout this sensory organ.

The ventral lobes are continued backward throughout the body and caudicle as the lateral nerve chords ("Seitenstämme"), fig. 1, *L.N.*, but do not unite posteriorly in an anal commissure.

The paired œsophageal nerves, fig. 16, *Oe.N.*, arise from the ventral lobes in the same frontal plane as the cerebral organs, but considerably ventral to them. A slender commissure, fig. 16, *Oe.N. Comm.*, is formed between them, .03 mm. behind their origin, outside the circular muscle layer, just anterior to the mouth, *M.* Behind the commissure the nerves pass through the circular and inner longitudinal muscle into the tissue around the mouth, occasionally giving off branches, and continue backward into the œsophageal region. Here they break up into numerous fine branches which ramify in the walls of the œsophagus, not only on the ventral side but also laterally, and which are very abundant on the dorsal side.

From the dorsal commissure arises the median unpaired upper

dorsal nerve, first termed by Hubrecht the "Rüsselscheidennerv," later the "medullary nerve;" by Bürger denominated the "oberen Rückennerv." The dorsal nerve extends throughout the body and ends about .06 mm. in front of the anal opening. No connection could be traced between the end of the dorsal nerve and the lateral nerves, but it is probable that a delicate plexus exists. The position of the dorsal nerve is constant, just above the circular muscle in the median plane of the body. A second dorsal nerve ("Rüsselscheidennerv," Hubrecht; "unterer Rückennerv," Bürger), separates off from the first shortly after its origin, passes inside the circular muscle of the body wall and lies just above the proboscis sheath. Both nerves are of fair size, about .017 mm. in diameter in the anterior part of the body, but both become much enlarged in the region of the muscular crosses between the greatly thickened inner circular muscle and that of the body wall, Plate XLI, fig. 23. Here for a short distance the diameter of the inner nerve reaches a thickness of .03-.06 mm. There is considerable variation in the respective sizes of the two nerves in different specimens. Sometimes the upper nerve is the larger one, but more often the lower nerve attains the greater size. The greatest size observed was in a specimen whose lower dorsal nerve measured .117 mm. dorso-ventrally and .058 mm. across; the upper dorsal nerve measuring .017 mm. in both directions. This enlarged condition coincided with the thickest part of the inner circular muscle layer. The same coincidence has been noted in the *Protonemertean*s and *Carinoma* by Hubrecht (1887), who says, p. 80: "The fact that in this (œsophageal) region of *Carinoma* the proboscidian sheath-nerve comes into the foreground so strongly that it might easily be mistaken for the medulla, may probably be ascribed to the massive development of the inner circular muscular layer δ , which in *Carinina*, *Carinella* and *Carinoma* acts at the same time as part of the wall of the proboscidian sheath. The fact was already noticed as a peculiar feature of the species by M'Intosh (1875), when he first described *Carinoma* (under the name of *Valencinia armandi*)." Posterior to the region of the inner circular muscle the two dorsal nerves resume their normal size, and then gradually decrease until they terminate near the end of the body.

Throughout the greater part of the body the lateral nerves are connected with each other and with the upper dorsal nerve by a

nervous layer of fibrous substance ("plexus" of Hubrecht, "Nervenschicht" of Bürger), situated outside the circular muscle. It is especially strong in the œsophageal part of the body, and in the inner circular muscle region, fig. 23, *n.p.* Posteriorly the layer is very thin, or may be entirely absent.

In one specimen a peculiar condition of the lateral chords was observed, Plate XLIV, fig. 62, *L.N.* A part of the fibrous substance extends toward the centre of the section in between the fibres of the circular muscle, *C.M.*; the fibres in the same radial line as the nerve are bent out of their course, and in the space thus formed is the apparent branch of the nerve, running inward. This condition was not confined to a few sections, but extended over several slides, a distance of at least 1.5 mm. It at first seemed as if a series of nerves was being given off from the inner lateral face of the nerve chord, instead of from the dorsal and ventral sides, the usual method in Nemerteans (Bürger). Several other specimens were examined, but this peculiarity was not found in them, and I am unable to account for it.

The proboscis is innervated by two slender branches that arise from the dorsal surface of the ventral commissure and immediately run dorsally into the proboscis, which is attached at this point to the body wall. The two proboscis nerves, Plate XLII, fig. 35, *P.N.*, are distinct in the anterior part of the proboscis, but in the "middle region," as will be described in that section, they become a continuous nervous layer, fig. 40, *n.p.*, separating again near the end of the proboscis into two distinct nerves, fig. 41, *P.N.*

b. Histology of Nervous System.—The brain lobes, as described by Bürger (1895) and Montgomery (1897 *b*), consist of (1) the fibrous core, (2) the inner neurilemma, (3) the ganglion cell layer, and (4) the outer neurilemma.

There is little to be said in regard to (1) and (2), as these structures in *Zygeupolia* conform to the usual Nemertean type.

In the ganglion cell layer of the brain occur the three types of nerve cells, the small, the medium-sized and the large, described by Bürger and Montgomery and denoted as I, II and III. Montgomery describes the cells of the first type, p. 385, as "densely massed together and of a shortened pyriform shape. The nucleus is very large in proportion to the cell body, in fact, nearly filling it" This description may also be applied to the cells of

the first type in *Zygeupolia*, figs. 20, 9, *G. C.*_I, which are found abundantly on the dorsal and outer lateral sides of the dorsal lobes, and on the outer lateral sides of the ventral lobes. They are very numerous around and in the cerebral organs.

The cells of the second type, figs. 20, 10, *G. C.*_{II}, are elongated and pear-shaped. The cytoplasm is more abundant than in I, the nucleus is oval and centrally placed, containing relatively less chromatin than that of I. These cells are arranged usually in radiate clusters, and their distribution in *Zygeupolia* agrees with that described for other Nemerteans by Bürger and Montgomery, namely, on the ventral lobes and along the lateral chords, never in the dorsal lobes.

The cells of the third type, figs. 20, 8, *G. C.*_{III}, are much larger than either I or II, but vary considerably in size. They are long, pear-shaped cells, with the greatest diameter proximally. The nucleus is large, round, and centrally placed, with a large nucleolus, and the chromatin distributed throughout the nucleus. Montgomery states that "while the cell bodies vary considerably in size, their nuclei remain of nearly uniform dimensions." These cells are found in both dorsal and ventral lobes and along the lateral chords.

A fourth type of cell has been discovered and named by Bürger (1894), namely, the colossal neurochord cells. Bürger (1899), p. 105, states: "Neurochordzellen fand ich bei allen von mir untersuchten Cerebratuliden, ferner bei *Langia formosa*. Das Gehirn besitzt stets nur ein einziges Paar von Neurochordzellen, welches an der medialen Fläche der ventralen Ganglien dort gelagert ist, wo die Schlundnerven entspringen. Zahlreiche Neurochordzellen befinden sich indessen im Ganglienzellbelag der Seitenstämme . . ." Bürger also found in the Metanemerteans *Drepanophorus* and *Prosadenoporus* one pair of neurochord cells in the brain, but none along the lateral chords. The presence of neurochord cells in *Cerebratulus lacteus* has been demonstrated by Montgomery (1897 b), who found that "the colossal ganglion cells (IV) of *Cerebratulus* are present in three pairs in the ventral brain lobes, and are distributed irregularly along the lateral chords, but are wholly absent in both ends of the latter (namely, in the oesophageal region and in the caudicle)."

In *Zygeupolia* a pair of large cells is found on the median sides

of the ventral brain lobes, about .06 mm. behind the ventral commissure. Both cells lie in the same transverse plane. In one very favorable specimen the nerve tubule of one cell could be traced into the fibrous core of the ventral lobe. These cells are elongated, with the greatest diameter at the rounded proximal end, and surrounded by a sheath of connective tissue fibres, Plate XL, fig. 3, *Cn. T.S.* The length of the cell body is about .058 mm., the greatest width about .029 mm., the diameter of the nucleus .012 mm. The cytoplasm stains a pale violet, hæmatoxylin and eosin stain, and has a slightly granular appearance. The somewhat oval nucleus is proximally placed, the chromatin is distributed around the periphery, and one large nucleolus is present.

From the position, size and structure of these cells it seems not unfitting to term them neurochord cells.

Bürger has observed that neurochord cells occur in those forms that swim freely, and he thinks there may be some correlation between the occurrence of neurochords and the swimming habit. While it would be hasty to say that *Zygeupolia* has not the power of free swimming, it has not been observed swimming; either in nature or in captivity. In its native habitat it is always found below the surface of the sand, and while in an aquarium it never rises to the surface, but remains on the bottom, burrowing in the sand, if there is any present, and surrounds itself as soon as possible with a slime sheath to which particles of sand adhere. When placed in a shallow dish of water the head is usually kept erect and continually swaying about, but there is little or no movement of the body as a whole.

It should be mentioned here that one pair of large ganglion cells, from their structure and position evidently neurochord cells, has lately been observed by the writer in *Micrura ewca*. It is not improbable that the occurrence of these cells among the Nemer-teans is more common than is generally supposed.

The outer neurilemma is but slightly developed in *Zygeupolia*. It is found around the ventral lobes, but does not occur to any extent around the dorsal lobes or along the lateral chords.

3. SENSE ORGANS.—*a. The Cerebral Organs.*—The cerebral organs appear in life, Plate XL, figs. 1, 16, (*C. Org.*), as rather pear-shaped bodies situated at the posterior ends of the dorsal brain lobes, above the ventral lobes. They are silvery gray, except the poste-

rior ends, which are dark greenish and contain large globules that have an oily appearance, the secretion from the posterior gland cells. The large blood vessels, in which the posterior ends of the cerebral organs lie, are very noticeable in life, fig. 16, (*C. Org. V.*) They are usually expanded, and the floating blood corpuscles may be seen even with a low power.

Each cerebral organ consists of the following parts: (1) the ciliated pit, opening directly to the exterior; (2) the ciliated canal, leading from the pit to the anterior end of (3) the cerebral organ proper.

The ciliated pit is the most anterior part of the cerebral organ. It is a flask-shaped cavity, lined with a ciliated epithelium that is differentiated histologically into several regions which will be described below. The pit opens directly on the surface of the head, there being no lateral slits, and in life is usually widely expanded, the long cilia beating vigorously. In fixed preparations the pit has a small external aperture, a narrow neck and the inner flask-shaped portion, Plate XLI, fig. 21, (*Cil. P.*)

The ciliated canal, *Cil. C.*, is a narrow duct, a continuation of the inner end of the ciliated pit. It extends in the transverse plane of the body from the ciliated pit to the anterior end of the cerebral organ proper, then, making a sharp turn at right angles to itself, it enters the cerebral organ and continues backward to the posterior end, where it terminates blindly.

The cerebral organ proper is a pear-shaped structure, wide at the anterior end and gradually becoming narrower at the posterior extremity. The cerebral organ nerve, which arises ventrally from the posterior end of the dorsal brain lobe, enters the anterior end of the cerebral organ on the dorsal surface, just in front of the entrance of the ciliated canal, and then ramifies throughout the organ.

The basement layer of the body epithelium is continued beneath the epithelium of the ciliated pit and forms around the cerebral organ an envelope of connective tissue, fig. 21, *Cn. T.S.*, of a thickness about equal to that of the inner neurilemma of the brain lobes. In fig. 21 the thickness of the basement layer and cerebral organ sheath is slightly exaggerated. The most anterior part of the cerebral organ is completely surrounded by muscular tissue—the inner longitudinal muscle on the inner surface, the circular muscle on the outer side.

The change in the relative position of the circular muscle in respect to the dorsal brain lobes and the cerebral organs has already been described, the circular muscle lying on the inner side of the dorsal lobe, but, with the beginning of the cerebral organs, bending out so as to adjoin their outer surfaces (cf. figs. 19 and 21).

From fig. 16 it may be seen that the cerebral organ vessels, *C.org. V.*, lateral branches from the median vessel, *M. V.*, run forward, partly encircling the cerebral organs and ending blindly near their anterior ends. The anterior part of the cerebral organ (see fig. 21, right side) is but partly surrounded by the blood vessel, while the posterior end,⁴ fig. 21, left side, lies nearly free in the blood vessel, being attached at the extreme tip to the body wall. A noticeable thinning of the connective tissue envelope accompanies the increase of the surface in contact with the blood vessel, and at its posterior end the cerebral organ is covered only by a low epithelium of square flattened cells, except at the point of attachment to the muscular wall, where a small portion of the connective tissue sheath persists, fig. 21, left side.

Histology.—The epithelium of the ciliated pit consists of three sharply differentiated regions: (1) the epithelium of the outer part, or the neck of the pit; (2) the epithelium lining the median part of the pit; (3) the innermost epithelium, adjoining that of the ciliated canal. These three regions may be seen in fig. 21, *Cil. P.* The epithelial cells have the same general structure in all three regions, except that the cilia of the cells in the median part (2) are much longer. A cell from the median part (2) is shown in fig. 7. It is a slender cell, with an expanded distal end on which the long cilia, *Cil.*, are borne, and tapering into a fine stalk at the proximal basal end; the small nucleus, *N.*, lies just above the stalk. Each cilium consists of a basal knob, an upper knob and a ciliary thread.

Between the ciliated supporting cells of the outer (1) and inner (3) regions, numerous large interstitial connective tissue cells are present, and their nuclei, fig. 21, *Cn. T. N.*, are very noticeable in sections. The median (2) region is characterized by its longer

⁴ The section drawn in fig. 21 is rather obliquely cut, so that on the right the plane of the section passes through the ciliated pit and the beginning of the cerebral organ, while on the left only the posterior part of the cerebral organ is seen.

cilia and the complete absence of the interstitial connective tissue cells. In a horizontal section of the ciliated pit the contrast between the three regions is very marked. In a preparation stained with hæmatoxylin-eosin, the outer and inner regions are studded with the deep-blue nuclei of the connective tissue cells, while the median region appears pink, from the cytoplasm of the supporting cells, their small nuclei being very inconspicuous.

The epithelium of the ciliated canal is a one-celled layer. The cells are much lower and wider than those of the pit and bear shorter cilia.

The anterior part of the cerebral organ proper, fig. 21, right side, is richly provided with gland cells, *Gl.*₁. These are large pear-shaped bodies with long slender ducts that open into the ciliated canal. The cytoplasm is abundant, especially at the base of the cell where the large spherical nucleus is situated. The secretion is homogeneous and stains red, hæmatoxylin-eosin stain.

The posterior part of the cerebral organ, fig. 21, left side, contains other gland cells of a different character, *Gl.*₂. The cytoplasm is inconspicuous, the nucleus is small, and the secretion has the form of large globules that stain a faint bluish-gray. These cells are prominent in life, evidently containing oily globules.

The cerebral organs are well supplied with nervous substance. Ganglion cells of the first type, fig. 21, *G. C.*₁, are very numerous.

b. The Lateral Grooves.—The lateral grooves are two shallow elongated pits extending horizontally, one on each side of the body, above the lateral nerve chords. Each has a length of about 1.5 mm.

The grooves are constant in position in the different specimens examined, always beginning at the posterior end of the *glandular zone*, Diagram 1, *Gl.Z.* and *L.G.*, and ending about 1.5 mm. in front of the great thickening of the inner circular muscle and the beginning of the middle intestine.

The lateral grooves are distinctly seen in cross sections of this region of the body, appearing as small pits or depressions in the epithelium external to each lateral nerve chord, but they are not macroscopically distinguishable in either living or preserved specimens, although they have been repeatedly sought. The shallowness of the grooves has probably rendered them indistinguishable except by the microscope.

The lateral areas of sections of the entire body have been carefully examined, but no indication of any constantly recurring depressions could be found in any other region of the body, either anteriorly or posteriorly. Here and there, of course, as in most Nemerteans, are small depressions of the surface due to contraction and shrinkage, but their extent is very limited, and they may occur in any position, dorsal, ventral or lateral.

Fig. 62 is a cross section of a portion of the body wall through one of the lateral grooves. It shows that the lateral groove, *L.G.*, is a depression both of the body epithelium, *Ep.*, and of the outer longitudinal muscle layer, *o.L.M.* The epithelial cells in the groove are rather closely crowded together, and the individual cells are not distinguishable with the magnification used. With a higher magnification, it may be seen that the epithelium is composed of supporting cells, gland cells and interstitial connective tissue cells, just like the rest of the body epithelium. There is no differentiation of the epithelial cells in the groove. Cutis gland cells of the blue-staining type, *Cu. GL.*, are present in the outer longitudinal muscle layer around the lateral nerve chord below the groove, and their ducts open between the epithelial cells of the groove.

The peculiar appearance of the lateral nerve, as shown in fig. 62, has already been discussed.

The question now to be considered is, What are the lateral grooves? Are they the result of contraction—*i.e.*, artifacts—or are they organs of the body?

The question whether the lateral grooves are merely contractions seems to me to be disposed of by the facts of their constant position, extent and regular occurrence in several individuals. The alternative, then, is that they are paired organs of the body; but with what function?

When these grooves were first observed, I believed that they were sense pits, comparable to the lateral sense organs ("Seiten-organe") of the Protonemerteans, and I hoped that further study, both upon living worms and sections, would demonstrate the presence of sensory cells and possibly of nerves.

The careful study of sections has not revealed any differentiations of the epithelial cells of the lateral groove, although no especial nerve technique, such as the Golgi or methylen blue

methods, has been employed. The possibility remains that under such treatment nerves and sensory cells may yet be demonstrated.

The strongest evidence in favor of considering the lateral grooves as sense organs is the fact that dermal sense organs—aside from the well-known lateral sense organs (“Seitenorgane”) of the Protoneurians, and the frontal organs of other forms—have lately been discovered in certain Nemertean.

In the anterior part of the body of *Parapolia aurantiaca* Coe⁵ there occur paired structures, resembling the lateral grooves of *Zygopodia*, and in the same relative position—that is, in the sides of the body posterior to the nephridia and anterior to the middle intestine. Plate XLIV, fig. 63, represents a transverse section of a part of the body wall of *Parapolia* through one of the lateral grooves. From this it may be seen that the outer longitudinal muscle, just outside the lateral nerve chord, contains an abundance of large swollen cutis gland cells, *Cu. GL.*. These cells stain blue with hæmatoxylin and are present only in the vicinity of the lateral nerves, being absent from the rest of the cutis. The section figured shows that the “lateral groove” is elevated above the general surface level, but in other sections it is depressed into a groove.

This elevation and depression of the “groove” is interesting when one recalls that, according to Bürger (1895), the Protoneurian lateral sense organs and the Metanemertean frontal organs may be both invaginated and everted. No differentiated sense cells or nerves are distinguishable in the “grooves” of *Parapodia*.

The length of the groove of *Parapodia* is about the same as that of *Zygopodia*, and they are probably homologous structures.

In the twelve dermal sense organs of the head, lately described by me (1900 *b*) for *Carinoma tremaphoros*, although undoubted sensory cells are present, only in one case could a nerve, running to the pit, be demonstrated.

The recent discovery of a pair of lateral sense organs in the new Heteronemertean *Micrella rufa* Punnett (1901 *b*) is of great interest and value. Punnett describes “a lateral sense organ on either side (fig. 2) shortly behind the excretory pore. In the pre-

⁵ Dr. Coe has very kindly allowed me to examine the slides of his type specimen of *Parapodia* and to make drawings of the sense organs. One of these is shown on Pl. XLIV, fig. 63.

served animal it is conspicuous as a small longitudinal slit (fig. 5) about .75 mm. long on either side. It is lined with characteristic glandular epithelium, resembling that found in the head slits (fig. 6).''

These facts suggest the possibility that the lateral grooves of *Zygeupolia* may be sense organs that are either in process of formation, or that have degenerated and lost their sensory character.

There remains one other interpretation of the lateral grooves, which has been suggested by the presence of the great *glandular zone* in front of the grooves and the situation of the gonads posterior to them. The glandular zone may have a function like the clitellum of the Annelids, and the lateral grooves may be like the grooves found along the sides of the body of an earthworm, and serve to conduct the mucous secretion to the egg cells. This last hypothesis could be substantiated only by a careful study of the habits of *Zygeupolia*.

4. THE RHYNCHODÆUM.—Immediately behind the tip of the head on the ventral surface may be found a very small opening, the proboscis pore ("Rüsselöffnung"), which is the external opening of the rhynchodæum.

The rhynchodæum is the rather cylindrical cavity that extends through the head from the point of attachment of the proboscis with the body wall, Plate XL, fig. 1, *y*, forward to the proboscis pore, *P.p.*, at the tip of the head. It is the path of exit for the evaginated proboscis.

A transverse section through the rhynchodæum shows that its walls are provided with four strong bundles of longitudinal muscle, seen in Plate XLI, fig. 18, *Rd.M.*, and that it is lined with a ciliated epithelium. This lining is very delicate and liable to be torn away, and usually can be seen only at the most anterior part of the rhynchodæum. It may persist farther back, but the cilia are mostly broken off in the preparations that have been sectioned. The cilia of this epithelial lining are considerably longer than those of the body epithelium.

5. RHYNCHOCÆL AND PROBOSCIS SHEATH.—The proboscis, fig. 1, *P.*, lies in a spacious cavity, the rhynchocæl, *Re.*, the muscular walls of which form the so-called "proboscis sheath." The rhynchocæl is closed anteriorly by the attachment of the proboscis to

the body wall, figs. 1, 16, *y*, and posteriorly ends blindly about .8 mm. in front of the anus, fig. 17, *Re*.

In the brain region the rhynchocoel is very narrow, passing between the dorsal and ventral commissures, fig. 20, *Re*. A constant widening of the rhynchocoel takes place in the oesophageal region, fig. 22, and the widest, most expanded part usually lies above that portion of the body extending from the nephridia to the beginning of the middle intestine (see fig. 1). At the latter point the great increase of the circular muscle layer of the proboscis sheath and of the inner circular layer causes a sudden constriction of the rhynchocoel, fig. 23. Posterior to this narrowed region, which is quite short, the rhynchocoel again widens, then gradually narrows more and more until near the end of the body the cavity is scarcely demonstrable.

The rhynchocoel is filled with a fluid in which float numerous long narrow cells, fig. 43, the "rhynchocoel corpuscles" of Bürger, "Navicula" of Quatrefages (1846) and Keferstein (1862). These cells are long and spindle-shaped, larger in the middle where the nucleus lies, and tapering to a fine point at each end. They are flattened and ribbonlike, as may be seen when the cell is twisted. Bürger (1892) has described an "attraction sphere" in the cytoplasm by the side of the nucleus. These do not appear in my preparations and, unfortunately, the rhynchocoel corpuscles were not studied in life. In one cell, however, the nuclear membrane curves in on one side, and a lighter zone in the adjoining cytoplasm may be seen, but there are no astral radiations. In another cell, fig. 43, *N*₁, two nuclei are present, probably the result of amitosis.

A second, smaller type of cell, fig. 42, is also found in the rhynchocoel, resembling the free corpuscles in the blood vessels. These cells are rounded, with finely granular cytoplasm and prominent nuclei.

The layers of the proboscis sheath are as follows (see figs. 20, 50):

1. The circular muscle layer, *C.M.p.s.*
2. The longitudinal muscle layer, *L.M.p.s.*
3. The basement layer, *B.L.*
4. The epithelium, *Re.Ep.*

The muscular layers are rather thin in the head region, except

when especially contracted. The basement layer is a homogeneous, gelatinous-looking, fibrous connective tissue layer, resembling that of the proboscis and body epithelia. The epithelial cells in the anterior part of the rhynchocœl, Plate XLIII, fig. 50, are not in close contact with each other and do not form a flattened endothelium. They are small, slender, pear-shaped cells, attached by their proximal ends to the basement membrane, with the nuclei at their distal ends, which project freely into the rhynchocœl. Farther back these cells become a flattened endothelium.

The dorsal blood vessel in this region is bordered on its ventral surface by numerous bundles of longitudinal muscle, evidently derived from the longitudinal muscle of the proboscis sheath.

From the end of the œsophageal region to the beginning of the middle intestine the rhynchocœl is usually greatly dilated, the proboscis is intricately coiled and much of the rhynchocœlomic fluid is centred here. Frequently the entire proboscis is drawn forward into this region, leaving the posterior part of the rhynchocœl quite empty.

The proboscis sheath in the expanded region is stretched to its greatest extent, so that it appears in cross section as an extremely thin sheet of tissue, and its component layers are scarcely distinguishable.

In the posterior part of the rhynchocœl—*i.e.*, in the part lying above the middle intestine—the circular muscle is the predominating layer in the proboscis sheath, the longitudinal muscle being represented by a very small number of fibres.

A word may be said here in regard to the comparative extent and character of the rhynchocœl and proboscis sheath in the different groups of Nemerteans, and of its position in respect to other organs.

In the Protonemerteans the rhynchocœl is short, its extent being only about one-third that of the body. It is widest in the nephridial region, then becomes constricted, owing to the thickening of the inner circular muscle, but again widens somewhat before its termination, just in front of the beginning of the middle intestine. In the words of Bürger (1895), p. 95: "Das Rhynchocœlom ist vor der Nephridialregion am geräumigsten, in derselben wird es durch die mächtig angeschwollene innere Ringmuskelschicht sehr beträchtlich eingeengt und erweitert sich wieder etwas, nach-

dem jene abgenommen hat, hinter den Nephridien." In *Humbrechtia* the rhynchocœl is short, ending just in front of the beginning of the middle intestine. To quote Bürger again, p. 106: "Der Mitteldarm von *H.* beginnt in der hinteren Region des Rhynchocœloms. In diesem vordersten Abschnitt des Mitteldarms erscheinen die Taschen nur als flache seitliche Ausbuchtungen des sehr geräumigen centralen Darmrohres. Sobald das Rhynchocœlom aufhört, verengt sich aber das centrale Rohr, und nunmehr werden die Taschen sehr umfangreich, sie erfüllen die Körper fast völlig."

Carinoma has the rhynchocœl extending throughout the body, but the character of the proboscis sheath is very diverse. In no other Nemertean is the inner circular muscle so highly developed, and as this muscle layer increases in thickness, the muscle of the proboscis sheath becomes thinner and finally disappears altogether. But with the ending of the inner circular muscle in the nephridial region, the proboscis sheath again acquires a musculature of its own. This region is also the beginning of the middle intestine—"Sowie der Vorderdarm aus dem inneren Ringmuskelschlauch herausgetreten ist, beginnt der Mitteldarm," Bürger (1895), p. 113. In *Callinera bürgeri*, Bergendal (1900 a), the rhynchocœl ends in the anterior part of the middle intestinal region by a great muscular swelling of its lateral and ventral walls. Bergendal, p. 314, describes this as follows: "Das Rhynchocœlom besitzt schwache Wände, bis dasselbe sich dem zweiten Drittel des Körpers nähert. Da erhält es zuerst eine sehr starke Grundschicht, die bald weiter nach hinten wieder verdünnt wird und in einen mächtigen Muskelsack eindringt. . . . Die dorsale Wand des Rhynchocœloms schwindet und besteht nur in einer etwas verstärkten Grundschicht. Die seitliche und ventrale Wand wird um so dicker und besteht aus sehr schönen bogenförmigen Muskelbändern . . . diese Schicht ist beinahe so mächtig wie die halbe Dicke des Körpers."

From these data it is seen that in Nemerteans with a short rhynchocœl, the termination of the latter is near the end of the nephridial region and the beginning of the middle intestine, and usually coinciding with the thickening, when present, of the inner circular muscle. *Carinoma* is no exception to this, for we may regard its long rhynchocœl as merely a secondary development backward

behind the usual point of termination. The same may be said of *Zygeupolia*. The expanded rhynchocoel is constricted in the region of the inner circular muscle at the beginning of the middle intestine, and instead of ending here, as may have been the case primitively, has secondarily developed backward through the whole length of the body.

6. THE PROBOSCIS.—The proboscis, Plate XL, figs. 1, 16, *P.*, is attached to the body wall in the brain region, just anterior to the dorsal commissure. It lies in the rhynchocoel, *Re.*, bathed by the rhynchocoelomic fluid. The posterior end is not attached to the wall of the rhynchocoel but is entirely free, there being no retractor muscle.

In regard to its histology the proboscis may be divided into three regions, which, however, pass very gradually into one another. These parts are (1) the anterior region, which is comparatively short, being of about the same length as the oesophagus, above which it lies; (2) the middle region, comprising the greater part of the proboscis; and (3) the extreme posterior region, only a few millimeters in length.

In the following description the nomenclature of Bürger (1895) will be followed, by which in the unevaginated proboscis the layers nearest the central cavity are termed the inner layers, those toward the periphery the outer.

The Anterior Region.—This part of the proboscis is usually straight and the average diameter is 0.116 mm. A cross section, Plate XLII, fig. 35, has the following layers:

1. The outer epithelium, *o.Ep.*
2. The subepithelial layer of circular muscle fibrils, *Ep.M.f.*
3. The outer basement layer, *o.B.L.*
4. The longitudinal muscle layer, *L.M.*
5. The lateral nerves, *P.N.*
6. The inner basement layer, *i.B.L.*
7. The inner epithelium, *i.Ep.*

The outer epithelium, fig. 44, *o.Ep.*, in the most anterior part of the anterior region, consists of low, rather brick-shaped cells, in which the cytoplasm is quite abundant, and whose nuclei are large and prominent. Farther back the cells are lower and finally form a flattened endothelium, that is frequently torn away in my preparations.

Just beneath the outer epithelium is a layer of very fine muscle fibres, *Ep.m.f.*, running circularly around the proboscis. These may be termed the subepithelial circular muscle layer⁶ of the proboscis. In a cross section of the proboscis, fig. 35, these fibrils are in longitudinal section, but in a longitudinal section of the proboscis, fig. 38, they are cut transversely, and it may be seen that the layer is only one fibril thick.

The basement layer, or ground substance, is a homogeneous, gelatinous-looking structure of considerable thickness. It is a product of the fibres of connective tissue cells, and their nuclei may be found scattered here and there among the fibres. The thickness varies considerably in different specimens. It may be most favorably studied in a specimen fixed with Gilson's fluid, one of the best fixatives for connective tissue. The region of the greatest thickness is always in the anterior part of the proboscis and rapidly diminishes toward the middle region.

The longitudinal muscle layer, *L.M.*, consists of bundles of fibres, about eight to ten fibres in each.

The two proboscis nerves, *P.N.*, are distinct from one another, each surrounded by a sheath of connective tissue.

The structure of the inner basement layer, *i.B.L.*, is similar to that of the outer layer but is only about one-third as thick. The inner epithelium, *i.Ep.*, is a one-celled layer. The cells are square in cross section, the cell-membranes distinct and the nuclei large and rounded. Between the epithelial cells are numerous gland cells, *Gl.*, the contents of which stain dark blue with hæmatoxylin. The central cavity of the proboscis is quite large in this region.

The transition stages between the anterior and middle regions are characterized by the decrease in thickness and the almost total disappearance of the outer basement layer. Its diminution is coincident with the establishment of a circular muscle layer on the axial side of the longitudinal muscle. A considerable amount of connective tissue appears within the new circular muscle layer, forming the core of the papillæ into which the inner surface of the proboscis is now raised. A considerable increase in the

⁶ The subepithelial muscle fibrils are not seen in fig. 44, which represents a portion of the proboscis only a few sections behind its point of attachment, but they begin a short distance farther back and form a continuous layer to the posterior tip of the proboscis.

height of the inner epithelial cells may be noticed, and gland cells are becoming more numerous.

The Middle Region.—The proboscis is usually greatly twisted and coiled, and the maximum diameter is found here, about 0.4 mm. The layers are as follows (see figs. 38, 40):

1. The outer epithelium, *o.Ep.*
2. The subepithelial layer of circular muscle fibrils, *Ep.m.f.*
3. The outer basement layer, *o.B.L.*
4. The longitudinal muscle layer, *L.M.*
5. The circular muscle layer, *C.M.*
6. The nervous plexus, *n.p.*
7. The connective tissue of the papillæ, *Cn.T.*
8. The inner epithelium, *i.Ep.*

1, 2, 3, 4 and 7 have essentially the same structure as in the transition stages. The notable features of this region are found in the circular muscle and the inner epithelium. Shortly after the appearance of the circular muscle layer, there is a crossing of the circular fibres at one point out through the longitudinal layer.

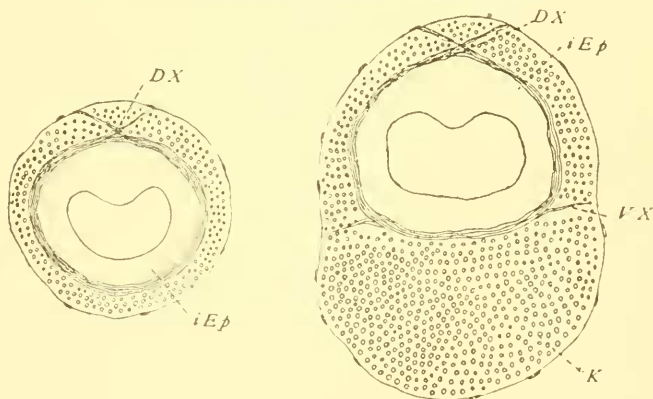


Diagram 6.—*Zygeupolia*, cross section of "middle region" of proboscis, with one muscular cross—*D X.*, dorsal muscular cross; *i.Ep.*, inner epithelium.

Diagram 7.—*Zygeupolia*, cross section of "middle region" of proboscis, with strong dorsal and faint ventral muscular cross—*D.X.*, dorsal muscular cross; *V.X.*, arm of ventral cross; *i.Ep.*, inner epithelium; *K.*, abnormal, enlarged region of longitudinal muscle.

The fibres of the cross are very thin, and after crossing are apparently continued as the subepithelial circular layer of fibrils before

described. It is a fact worthy of note that although the crossing of the circular fibres takes place first in the middle region, the subepithelial layer of circular fibrils extends almost to the anterior end of the proboscis.

In some specimens the muscular cross is present on the dorsal surface only (see Diagram 6, *D.X.*), in others there is a weaker cross on the ventral side, fig. 40, and in still other specimens the two arms of the ventral cross are very faint, and lie about 120° apart (see Diagram 7, *V.X.*). In this latter case there is an exceptional arrangement of the longitudinal muscle fibres of the proboscis. The dorso-ventral diameter is about .145 mm., and almost one-half of the area of the proboscis is occupied by the circular muscle of the ventral side, Diagram 7, *K.* The muscle fibres have increased enormously on this side, and spaces filled with a connective tissue reticulum separate the wide part of the layer from the narrower, normal part. Through these connective tissue areas run the fibres of the ventral cross.

The lateral nerves are separate at the beginning of the middle region, but farther back they spread out into a thin nervous layer, fig. 40, *n.p.*, which forms a continuous ring around the proboscis, along the inner surface of the circular muscle.

The glandular inner epithelium of the middle region is characterized by a structure that will be termed the *glandular ridge*, Plate XLII, fig. 40, *GLR.* The dorsal surface bears an elevation consisting of a core of connective tissue, *Cn.T.*, which is continued throughout the middle region. The epithelium clothing the ridge is very specialized. The entire surface of the ridge is thrown into a series of lesser elevations, or knobs, covered by masses of rod-shaped bodies that are aggregated in clusters, each cluster on a small papilla. With hæmatoxylin-eosin these rods stain a bright red, and are evidently glandular secretions. Bürger (1895) has described and figured, from the probosces of living worms, very similar structures, which he has termed rhabdites. Bürger considers each rhabdite as the product of a single cell. As the red-staining bodies in *Zygeupolia* bear a close resemblance to the rhabdites of Bürger, they will receive the same term. Unfortunately the proboscis of *Zygeupolia* was not studied in life, so that the descriptions here given are based wholly on sections.⁷

⁷ The best fixation for the rhabdites is 95 per cent. alcohol; their structure is also shown, but not so well, with corrosive sublimate and 50 per cent.

Fig. 36 shows a small branch of the glandular ridge, on the surface of which are several clusters of rhabdites. The section has passed through the centre of the branch, exposing the central connective tissue core, the lightly shaded area, *Cn. T.* No nuclei have been seen in the rhabdite cells, probably owing to the great number and the close proximity of the glandular secretions.

The inner epithelium of the ventral surface is of quite a different character. A certain amount of interstitial connective tissue is present at the base, but there are no elevations. The most prominent constituents of the epithelium are the large pink-staining (hæmatoxylin-eosin) gland cells, fig. 40, *Gl.*₁. These cells are quite elongated, the distal ends are large, and the proximal ends are narrowed into a slender stalk. The cell body is entirely filled with the granular secretion, and the nucleus lies just above the stalk. Between the gland cells are very slender cells, somewhat resembling epithelial supporting cells in shape. The nucleus is at the base of the slender cell body, and in the distal cytoplasm may be found one, or sometimes two, rods shaped like a thorn, with flat base and pointed end. The base is embedded in the cytoplasm, the pointed ends project beyond the cell. These structures, fig. 40, *Th.*, stain a deep blue, hæmatoxylin-eosin; brownish with the Ehrlich-Biondi stain.

The Posterior Region.—The diameter of the proboscis in the posterior region, fig. 41, is constantly decreasing, until at the extreme tip it measures only .04 mm.

The outer epithelial cells, fig. 39, *o. Ep.*, like those of the extreme anterior region, are rather brick-shaped cells with abundant cytoplasm, and do not form a flattened endothelium. The muscle layers have decreased relatively to the other tissues; and instead of the nervous plexus of the middle region, there are, again, two separate lateral nerves, *P. N.* The amount of connective tissue, *Cn. T. N.*, has increased, and as the nuclei of these cells are large, with but little cytoplasm, the effect produced is that of a layer of undifferentiated tissue. The glandular ridge has disappeared, and the inner epithelium is of a uniform character, consisting of pink-staining gland cells, *Gl.*₁, like those in the ventral epithelium of the middle region.

alcohol; while they are swollen and quite unrecognizable with Flemming's fluid.

At the extreme tip of the proboscis the muscular layers almost disappear, the connective tissue cells become even more abundant, and the gland cells of the inner epithelium are replaced by low, flattened endothelial cells.

7. THE BLOOD VASCULAR SYSTEM.—The anterior part of the head of *Zygeupolia* differs from that of most Nemerteans in being quite devoid of blood vessels, and even of blood spaces that are large enough to be seen, although there is no doubt a network of capillaries too fine to be distinguishable either in life or in fixed preparations.

The blood system makes its first appearance in the brain region, just behind the insertion of the proboscis, Plate XL, fig. 16.

In the blood system the following parts may be found (see figs. 16, 17):

(1) The fine paired head vessels, *H. V.*,^{*} which unite to form (2) the unpaired median vessel, *M. V.*; (3) the paired cerebral organ vessels, *C. Org. V.*; (4) the unpaired dorsal vessel, *D. V.*; (5) the paired lateral vessels of the body, *L. V.*; (6) the ventral connectives of the lateral vessels (fig. 22), *V. bl. con.*; (7) the paired dorso-lateral vessels at the posterior end of the body, derived from the forking of the unpaired dorsal vessel, *Dl. V.*, and (8) the central blood lacuna in the caudicle, *Bl. L.*

In sections of the brain region, fig. 19, *H. V.*, the head vessels appear as two irregular clefts running dorso-ventrally, one on each side of the proboscis, just behind its insertion. These narrow slits lie in the limited area between the proboscis sheath and the circular muscle of the body wall, and in the vicinity of the ventral brain commissure their ventral ends coalesce, forming an unpaired crescent-shaped vessel, the median vessel, which encircles the lower half of the proboscis sheath, fig. 20, *M. V.*

The median blood vessel extends from this point backward as far as the mouth. In its course it becomes considerably deeper dorso-ventrally, and is very noticeable in sections of this region. It assumes a horseshoe shape, with the apex pointing ventrally and the two long slender arms prolonged dorsally. In the vicinity of the cerebral organs, fig. 21, the arms are cut off by a horizontal band of muscle fibres, *II. M.*, that lies beneath the cerebral organs

^{*} The reference line from *H. V.*, in fig. 16, should extend in as far as the red lines indicating the head vessel.

and the rhynchocoel, so that only the triangular middle part of the median vessel now remains.

Immediately behind the ventral brain commissure the unpaired dorsal blood vessel arises from the median vessel, figs. 16, 21, *D. V.* It passes up through the muscle layers of the proboscis sheath into the rhynchocoel, and continues in this position—on the floor of the rhynchocoel in the median line, but bounded dorsally by the rhynchocoelomic epithelium—until about the middle of the nephridial region, fig. 22. Here the dorsal vessel passes down through the proboscis sheath and out again into the tissue that is just beneath the rhynchocoel and above the alimentary canal; and this position is retained throughout the remainder of its course, figs. 23, 24.

In the anterior œsophageal region the lateral blood vessels are united beneath the œsophagus by ventral connectives. In one specimen the connectives are broad and dilated, fig. 22, *V.bl.con.*, in others they are almost entirely shrunk together. The ventral connection of the lateral trunks is continued throughout the œsophageal region, forming a network of fine anastomosing branches. It is probably further continued, in the remainder of the body, but I have been unable to follow it in my specimens.

In the œsophageal region the lateral trunks lie on the dorso-lateral side of the alimentary canal; in the middle intestinal region they have moved ventrally and lie on the ventral side of the intestine.

No connection between the dorsal vessel and the lateral trunks has been observed, except at the extreme posterior end of the body. Some little distance in front of the end of the body proper (see fig. 17) the dorsal vessel divides into two, which for a time lie side by side, their walls adjoining. They then move apart, and lie in about the same relative distance from one another as do the two ventral lateral trunks, so that in a section of this region, fig. 26, four vessels are present, symmetrically placed.

Just anterior to the anal opening the two dorsal vessels, or rather the dorso-lateral vessels, descend and unite with their ventral fellows in a large blood lacuna, fig. 27, *Bl.L.* This lacuna now occupies most of the area inside the body musculature, for the intestine curves dorsally and shortly opens to the exterior on the dorsal surface of the body. The large lacuna passes on into the caudicle, fig. 17, *Bl.L.*, and continues throughout its length. It has no definite walls, but is bounded by the muscular wall of the caudicle, on the

inner surface of which are irregular groups of large mesenchym cells, figs. 27, 28, *mes.*, many of which become detached and float freely in the lacuna.

Histology.—The wall of the median blood vessel is a one-celled layer, fig. 29, of low, somewhat flattened cells that are wider than high. The nuclei are oval and rather prominent and the cytoplasm clear and hyaline. In places the wall becomes a flattened endothelium, often appearing in cross section like a thin membrane, along which the nuclei lie.

The lining of the cerebral organ blood vessels is of a similar character.

The dorsal blood vessel, as already mentioned, lies, in the anterior part of its course, in the mid-ventral wall of the rhynchocœl, and posteriorly, beneath the rhynchocœl.

Fig. 50, a section through the dorsal blood vessel shortly behind its origin, shows that the vessel is surrounded ventrally and laterally by bundles of longitudinal fibres, which are more numerous here than on the other surfaces of the rhynchocœl wall, and probably take part in the contractions of the vessel, while the dorsal surface of the vessel is bounded by the epithelial lining of the rhynchocœl, *Rc. Ep.*

The wall of the dorsal vessel consists of an endothelium, *End.*, of low, rather brick-shaped cells with large nuclei. The cells of the ventral part of the wall are very regularly arranged, Plate XLIII, fig. 50, but the regularity of the dorsal wall is interrupted by the proliferation of numerous blood-forming cells, *Bl.f. C.*, that project into the lumen of the vessel and remain for some time attached to the dorsal wall by their slender stalks.

The boundary between the dorsal wall of the blood vessel and the epithelium of the rhynchocœl is marked by a fine line, *Bl. M.*, that varies in distinctness in different preparations. After the hæmatoxylin-eosin stain it appears pink, after iron-hæmatoxylin, black, so that it is probable that a few muscle fibres are present here, forming a very delicate circular layer around the dorsal side of the vessel. This line might also represent a deeply stained connective tissue layer, but, since the dorsal vessel after leaving the rhynchocœl has a well-defined muscle sheath, it seems more likely that this is the beginning of a muscle layer.

The blood-forming cells are evidently enlarged endothelial cells,

that gradually separate off and become free. At first pear-shaped, with a slender stalk, they later become rounded and are frequently amoeboid in outline, fig. 51, *Bl.f. C.* The cytoplasm is finely granular in appearance and quite prominent. In the anterior (rhynchocoelomic) part of the dorsal vessel the blood-forming cells arise only from the dorsal side, but posteriorly from all sides of the dorsal vessel (cf. figs. 50, 51).

The dorsal blood vessel after leaving the rhynchocoel lies beneath it and above the intestine, figs. 22, 23, immediately surrounded by a network of connective tissue cells. The wall, fig. 51, consists of an inner endothelium, *End.*, and an outer circular muscle layer, *Bl.M.*, that in this region is continued around the entire vessel, and is not confined to the dorso-lateral surface, as in the anterior region. The muscle fibres are very fine, but are clear and distinct, and are especially well seen in tangential sections of the vessel. The endothelium, *End.*, is very irregular, being interrupted by the proliferation of cells from all sides of the vessel. In places, many consecutive sections of the vessel may be examined without finding a single true endothelial cell, while numerous blood-forming cells are present in each section. Two explanations for this are possible: either all the endothelial cells have been changed into blood-forming cells, or the endothelium has been rubbed or torn off. The latter is supported by the fact that a thin lining of cytoplasm may nearly always be seen on the inner side of the muscular layer, even though no nuclei are present.

The two dorso-lateral vessels at the posterior end of the body, figs. 26, 49, have the same histological structure as the dorsal vessel—the outer, circular muscle layer, and the inner, more or less interrupted endothelium and numerous blood-forming cells.

The lateral vessels, figs. 46, 47, *L.V.*, and their ventral connectives, *V.bl.con.*, are lined anteriorly by low, brick-shaped cells like those of the median vessel, with prominent nuclei and hyaline cytoplasm. This endothelium soon becomes more flattened and membranous. Here and there a blood-forming cell is given off, fig. 46, *Bl.f. C.*, but there is no abundant proliferation of these cells as in the dorsal vessel. In the nephridial region the endothelium of the lateral blood vessels is discontinuous, being absent from the surfaces of the terminal bulbs. No muscular layer is present in the anterior part of the lateral vessels, the wall consist-

ing merely of the endothelium. Outside of the membranous endothelium, in the more posterior part of the lateral vessels, fine fibrils are seen. These may be either fine muscular fibrils, or the end processes of the branched connective tissue cells that are so numerous around the blood vessels. From their general appearance, and from the absence of muscle fibres in the more anterior part of the lateral vessels, I am inclined to regard them rather as connective tissue fibres.

8. THE EXCRETORY SYSTEM.—The paired nephridia,⁹ fig. 1, *Nph.*, lie in the anterior part of the body, about 6–7 mm. behind the mouth, bordering on the ventral surface of the lateral blood vessels and running parallel with them; they are about 2.5 mm. in length, and there is no communication between the two nephridia. Each nephridium may be briefly described as a slightly convoluted tube (the main duct) that opens to the exterior by a narrow duct (excretory duct) at its posterior end, and which anteriorly gives off a number of slender, thin-walled branches (the ductules), each of these ending blindly in a group of specialized cells, known as a terminal bulb (“Endkölbchen,” Bürger).

The most anterior part of the nephridial system, consisting of the terminal bulbs, fig. 47, *T.B.*, and their ductules, *Nph.d.*, is found along the ventral surface of the lateral blood vessels, *L.V.*, and their ventral connectives, Plate XLI, fig. 22, *V.bl.con.* No main duct is present in this region, and the irregular network of the fine ductules and their blind ends at first seemed a hopelessly confused mass of tissue, but by the careful study of serial sections the relative arrangement of the parts has been made out.

The terminal bulb, Plate XLIII, fig. 47, *T.B.*, is the blind enlarged end of the fine ductule, *Nph.d.*, coming from the main duct, fig. 46, *Nph.D.* Each bulb consists of a number of cells, probably eight to ten or more, but it is difficult to determine this exactly as a bulb does not always lie wholly in one section. The cells of the bulb are placed side to side about a central lumen, so that the walls of the bulb are one cell thick. The height of the cells—that is, the

⁹Several attempts were made to study the nephridia in life, but they could be seen in two specimens only. In these, merely the presence of the main duct was made out, and in one case the excretory duct. The methylene blue method, employed by Bürger (1892, p. 327, footnote) for the study of the nephridia of *Eupolia* and various Metanemertans, was tried but without success, so that the following description is based entirely upon the study of sections.

distance from the lumen to the periphery of the bulb—is greater than their width. The peripheral ends are considerably enlarged and often irregular in outline; the luminal ends are frequently produced into long slender processes that seem to take some part in the formation of the stem of the bulb. The cytoplasm of the peripheral (proximal) end takes a bright pink, hæmatoxylin-eosin stain; the distal processes, however, stain very faintly. The nucleus is large and fusiform, but appears round in cross section, and is situated in the expanded proximal end of the cell.

After finding the terminal bulb cells so well preserved in sections, it seemed most probable that the long branches of vibratile cilia, the "ciliary flames" ("Wimperflammen," Bürger), present in the terminal bulbs of other Nemerteans, might also be found; but although they have been carefully looked for, they have not been seen. Cilia, fig. 46, *Cil.*, are found on the cells of the nephridial duct and of the ductules, and generally in a good state of preservation, so that it seems improbable that the cilia of the bulbs should have been destroyed by fixation. On the other hand, the analogy with the terminal bulbs of those Nemerteans that have been exhaustively studied is in favor of their presence in *Zygopolia* also.

The bulbs project freely into the blood vessel all along its ventral surface, and in one case a ductule was observed that passed through the vessel, so that its bulb came to lie on the opposite, dorsal, surface. The epithelial lining of the blood vessel is frequently broken and discontinuous in the region of the bulbs, figs. 46, 47, and in no place are the bulbs covered by it, so that the ends of the bulbs are directly bathed by the blood. The absence of the blood vessel epithelium from the ends of the bulbs may facilitate the absorption of waste substance from the blood, and this may account for the disappearance of the lining from around the bulbs of the nephridia.

No internal openings between the nephridium and the blood vessel, such as Oudemans describes in *Carinoma armandi*, have been seen.

The nephridial ductules, figs. 46, 47, *Nph.d.*, the slender tubes that connect the terminal bulbs and the main duct, are very sinuous, and it is probable that several terminal bulbs may connect with one ductule. Some ductules are quite long, especially those

that run along the ventral blood connectives. The wall of the ductule is a one-celled layer and encloses a narrow lumen. The cells are wider than high, with but little cytoplasm and elongated nuclei. The cell surface turned toward the lumen bears cilia. No basement membrane is present.

About 3-4 mm. behind the first appearance of the terminal bulbs the main nephridial duct begins, fig. 46, *Nph.D.* It is situated on the ventral side of the lateral blood vessel, in the angle made by the junction of the ventral connective with the lateral vessel; the main duct does not project into the blood vessel, but merely adjoins it with one surface, the other surfaces being surrounded by the fibres of the inner longitudinal muscle layer. The main duct is about 2 mm. long and composes the greater part of the nephridium. Into its anterior end for some little distance the ductules open, but behind that there are no diverticula until the excretory duct at the posterior end is reached. The main duct is thick-walled, fig. 46, and slightly convoluted throughout its length. The cells of the wall are considerably higher than wide, with quite sharply defined cell membranes. The nuclei are prominent and are situated near the outer or basal side of the cell, *i.e.*, away from the lumen of the duct. The outer surfaces of the cells are usually irregular, and often bear amœboid processes, no basement membrane being present. The surface bordering on the lumen is ciliated, and the basal knobs of the cilia are very distinct.

In the cells of the main duct and ductules of one specimen that had been fixed in a solution of sublimate in 50 per cent. alcohol, and stained with hæmatoxylin and eosin, were found numerous prominent red-staining bodies of the same size as the nucleus, but neither larger nor smaller ones. Wherever these red bodies occurred they were found one to a cell, and at first it seemed as if they were degenerating nuclei. Careful examination, however, detected the nucleus in each cell, of normal size, but staining less deeply than usual. It is possible that these bodies may be excretory masses, but their absence from the lumen of the duct and the fact that no intermediate stages in their formation have been seen would discredit this view. Bürger (1890), p. 93, describes in the nephridia of *Carinella* what may be similar masses: "Schon in den Zellen der . . . Endkanälchen und Endkolben, fielen mir bis kerngrosse glänzende grüne Konkreme

auf. Ueber ihre Natur musste ich im Unklaren bleiben; niemals beobachtete ich solche im Excretionsgefäßslumen selbst."

The excretory duct, figs. 1, 45, *Exc.d.*, is the small, thin-walled tube that connects the main duct with the exterior. Its course is in a plane at right angles to the plane of the main duct, and it opens to the exterior just dorsal to the lateral nerve chord. Since the excretory duct runs in a direct line to the epidermis with but little turning or twisting, its length is merely the distance from the main duct to the surface of the body wall. The cells composing the wall are much lower than those of the main duct, and are wider than high, the height being about .006 mm. Cilia are borne on the inner surface. No basement membrane is present. The cells of the excretory duct meet those of the body epithelium at the surface of the body, there being little or no invagination of the epidermis.

A good deal of evidently foreign matter from the exterior is usually found in the excretory duct.

9. THE ALIMENTARY SYSTEM.—The alimentary canal of the Heteronemerteans is usually divided into the following regions: (1) The mouth; (2) the œsophagus, or anterior intestine ("Vorderdarm," Bürger), a straight tube without lateral diverticula; (3) the middle intestine ("Mitteldarm," Bürger), with lateral outgrowths or cæca throughout its length; (4) the anal portion of the intestine ("Enddarm"), a short region where the lateral cæca are no longer present, terminating in (5) the anal opening. Bürger (1895), p. 240, says: "Wir nennen den ungegliederten vorderen Darmabschnitt Vorderdarm, den gegliederten, welcher der mittleren und hinteren Körperregion charakteristisch ist, den Mitteldarm. Wir bezeichnen ferner am Mitteldarm den röhrenförmigen Theil als axiales Rohr, die peripheren Ausstülpungen desselben als Darmtaschen."

According to Bürger, the œsophagus (Vorderdarm) has frequently two regions, an anterior and a posterior, that differ histologically from one another. In *Carinella* Bürger finds the epithelium of the anterior part of the "Vorderdarm" very rich in gland cells, while the posterior part consists mostly of supporting cells with a few scattered gland cells; and in *Cerebratulus marginatus* he finds the same differentiation of anterior and posterior parts,

only in this genus the anterior glandular part is more extensive than the posterior part. Bürger's own words, p. 250, are: "Im Vergleich mit *Carinella* setzt sich das Drüsenepithel der Mundhöhle, welches dort ja ganz ähnlich wie bei *Cerebratulus marginatus* beschaffen ist, aber nur die Mundhöhle und den allervordersten Abschnitt des Vorderdarms auskleidet, bei den Cerebratuliden weit nach hinten fort. . . . Aber es fehlt auch nicht jener zweite Abschnitt des Vorderdarms bei *Cerebratulus*, welcher sich durch seine Drüsenzellen wesentlich von dem ersten unterscheidet und den Uebergang in den bei den höheren Formen durch die Darmtaschen auch morphologisch von dem vorderen Darmabschnitt differenzirten Mitteldarm bildet. . . . Es giebt also bei *Cerebratulus*, just wie bei *Carinella*, einen äusserst drüsenreichen vorderen und einen auffallend drüsenarmen hinteren Vorderdarmabschnitt."

In *Zygeupolia* the differences between the anterior and the posterior parts of the tube-like portion of the alimentary canal (Vorderdarm) are so great that in this description the two parts will be termed respectively the œsophagus and the stomach. My reasons for this are partly for the sake of brevity and clearness, since the expressions "anterior part of anterior intestine" and "posterior part of anterior intestine" are lengthy and awkward to use; and partly to emphasize the very considerable differences in the structure of the two regions. It is my belief that while the œsophagus is evidently derived from the ectoderm, the stomach, together with the middle intestine, owes its origin to the entoderm. The term stomach is not altogether a happy one, since it at once suggests the "Magendarm" or stomach intestine of the Metanemerteans, which may have a different embryological history; and yet, on the other hand, the function of both is evidently digestive, and the resemblances in the histology very striking. Both have a truly glandular epithelium, as will be seen by comparing the section of the epithelium of the "Magendarm" of *Drepanophorus latus*, figured by Bürger (1895), Taf. 27, Fig. 17, with the epithelium of the stomach of *Zygeupolia*, Plate XLII, figs. 32, 33.

Therefore, in *Zygeupolia* the alimentary canal will be subdivided into the following regions (see fig. 1): (1) The mouth, *M.*; (2) the œsophagus, *Oes.*; (3) the stomach, *S.*; (4) the middle intestine, *M.I.*; (5) the end intestine, *E.I.* (Euddarm), and (6) the anus, fig. 17, A.

The mouth, figs. 1, 16, *M.*, is situated on the ventral surface of the body, shortly behind the brain, and about 5 mm. from the tip of the head. In a passive condition the mouth is a small round opening, with crinkled edges forming a kind of circular lip, but it is capable of great expansion, enabling the worm to swallow prey nearly as large as itself. The tissue immediately encircling the mouth is conspicuous in life by its greenish hue, caused by the secretions of the numerous gland cells, figs. 16, 31, *w.*, that are situated in the subepithelial tissue of the anterior œsophageal region.

A cross section of the body through the mouth opening shows that the mouth is lined with an epithelium of ciliated supporting cells resembling those of the body epithelium, but with longer cilia. No gland cells could be distinguished in the epithelium of the mouth-opening proper, nor in the cutis beneath it.

In the semi-transparent living *Zygeupolia* the œsophagus and the stomach may be easily seen under a low power in a slightly compressed specimen. The different degrees of refraction of the two parts makes them easily distinguishable. The œsophagus, fig. 1, *Oes*, appears rather light, while the stomach, *S.*, is darker, denser and of a more granular appearance. It will be seen from fig. 1 that the œsophagus is rather shorter than the stomach. These two regions do not pass gradually into one another, but there is a sudden transition which might be indicated by a straight line drawn at right angles to the long axis of the alimentary canal (see fig. 1), and sections show that there is an abrupt change in the cell elements. In life there is an appearance of a fold at the beginning of the stomach, which probably serves as a valve.

Fig. 33 is a somewhat oblique cross section of the alimentary canal through the line of division of œsophagus and stomach. The slight obliquity takes the section through both œsophagus and stomach; the œsophageal epithelium, *Oe.Ep.*, being present on the ventral surface, the stomach epithelium, *S.Ep.*, on the dorsal surface. In the upper right hand part of the figure indications of a fold, *f.*, are seen, where the œsophageal epithelium apparently passes over the stomach epithelium.

The beginning of the stomach has a constant relative position, occurring always in the same frontal plane with the anterior nephridial region (see fig. 1). This fact is helpful in trying to find the nephridia in life.

The œsophagus extends backward from the mouth a distance of about 9–12 mm., according to the size of the worm. The wall of the œsophagus, figs. 31, 33, consists of an epithelium of ciliated supporting cells, *S.C.*, and gland cells, *Gl.*, about .023 mm. in height, very similar to that of the epidermis (cf. figs. 2 and 31). The supporting cells are like those of the epidermis, only more slender. The gland cells are flask-shaped, with finely granular contents that stain a bright pink, hæmatoxylin-eosin stain. Blue-staining gland cells are entirely absent. Both supporting and gland cells rest on a delicate basement membrane, *B.M.*, and some interstitial connective tissue cells are found between the bases of the epithelial cells.

At the extreme posterior end of the œsophagus some of the epithelial cells become much higher, but otherwise their structure is the same.

The subepithelial gland cells, that have been described above as giving the greenish color in life to the circular "lip" of the mouth, are present in great numbers immediately around the mouth, and less abundantly throughout the greater part of the œsophagus. A group of these cells, *w.*, is shown in fig. 31, from the anterior part of the œsophagus. The gland cells are large, the cell body containing a secretion that is probably fluid in life, but appears finely granular in the fixed preparations and stains rose red, hæmatoxylin-eosin stain. Some cells seem to have but one nucleus, others more than one, but the latter case may be due to the crowding together of the cells or to the presence of the adjacent connective tissue nuclei, so that this point has not been definitely settled. The ducts, *dt.*, are long and slender, and open into the œsophagus between the epithelial cells. Farther back in the œsophagus these subepithelial gland cells entirely disappear.

The inner surface of the œsophagus is usually thrown into numerous high papillæ, especially the ventral surface (see fig. 33). The papillæ are formed chiefly of longitudinal muscle fibres, but contain also connective tissue cells and the subepithelial gland cells, when they are present. The papillæ come to an end together with the œsophagus (cf. the dorsal and ventral surfaces of fig. 33).

A few isolated strands of circularly running muscle fibres, fig. 33, *M.S.*, are frequently found beneath the papillæ, partly encircling the œsophagus, but no continuous "œsophageal" muscle

layer is formed. The origin of these strands has been traced in some cases to the circular muscle of the proboscis sheath, in other cases to dorso-ventral fibres coming from the outer circular muscle of the body wall.

The change between the œsophagus and stomach is not only a sudden but a very marked one (see fig. 33). Instead of the œsophagus, with its low epithelium and its great extent of surface caused by the high papillæ, there is the stomach, without folds or papillæ and consisting of a very high epithelium, about four times higher than that of the œsophagus, in which the large gland cells are the principal element. The ciliated supporting cells, *S.C.*, are present, apparently in equal numbers with the gland cells, but are so small and inconspicuous that they are easily overlooked. In fact, four specimens were studied before their presence was detected, and they were seen for the first time in an overstained specimen, where the deep blue stain taken by their cytoplasm and their ciliary bases was in strong contrast to the pink of the adjacent gland cells.

The gland cells of the stomach, fig. 32, *GL*₁, are large, measuring .087 mm. in height and .011 mm. in width. The distal end is slightly narrowed into a neck, and the basal end into a slender process that is inserted into the basement membrane, *B.M.* The cell membrane is very distinct, and the cell body is filled with a network of cytoplasm, in which are embedded large homogeneous secretion globules that stain pink with eosin. Some slight color differences seem to indicate different phases in the secretion, and a few cells appearing lighter in color had evidently discharged most of their secretion. The rather small oval nucleus, *N.*, lies near the base of the cell, not far above the basal process.

Alternating with the gland cells are the small ciliated supporting cells, fig. 32, *S.C.* They have a small cell body, about .004 mm. in width, on a very long stalk, *St.*, the basal ends of which are inserted into the basement membrane. The cilia are short and their structure could not be determined. A surface view of these cells shows that there is one stout cilium in the middle of the cell, while the other more slender ones are arranged in a ring around the periphery of the upper surface. The stouter cilium may occasionally be seen in sections, and then appears slightly longer than the peripheral ones. A few small interstitial connective tissue

cells are present among the bases of the gland and supporting cells, and are demonstrable chiefly by their nuclei.

The basement membrane of the stomach rests directly upon the inner longitudinal muscle of the body wall. The stomach is frequently greatly flattened by the pressure exerted by the expanded rhynchoœel. For the study of this region, a specimen from which the proboscis has been cast out is the most favorable.

The middle intestine, *M.I.*, according to definition, begins with the first pair of lateral intestinal cœca, but the cells that are peculiarly characteristic of the middle intestine are not found in the most anterior cœca or pouches, which are lined by cells similar to those of the stomach. In other words, the most anterior pouches of the middle intestine belong histologically to the stomach.

The transition from the gland cells and ciliated supporting cells, exactly similar to those of the stomach, that are found in the most anterior pouches, to the absorptive cells characteristic of the middle intestine is a very gradual one, and varies in different individuals. In some specimens the transition begins in the second pair of cœca, in others it takes place farther back. There is no abrupt line where gland cells end and absorptive cells begin, like the sharp line between the end of the œsophagus and the beginning of the stomach, but the gland cells and their companion supporting cells gradually become less numerous and are replaced by the absorptive cells that belong to the middle intestine. Throughout the course of the middle intestine, here and there are found gland cells, fig. 34, *Gl.*₁, just like those of the stomach and the anterior pouches.

It is the presence of these gland cells, characteristic of the stomach, in the anterior pouches and scattered through the rest of the middle intestine, that has led me to believe that probably the stomach and the middle intestine have a common origin from the entoderm. The fact that there is not a well-defined histological dividing line between the cell elements of the two regions, but a gradual replacement of the gland cells by the absorptive cells, is in confirmation of this opinion. And furthermore, to return to the differences between œsophagus and stomach, here we do find a sharply defined and sudden transition from an epithelium resembling that of the outside of the body to a truly glandular epithelium; also, the opening to the stomach provided with a primitive

valvular fold. Here is certainly the division line between ectodermal and entodermal derivatives.

The characteristic absorptive cells of the middle intestine, fig. 34, *Abs. C.*, are long slender cells, about .14 mm. high, rather flattened at the base and inserted by slender lateral processes into the basement membrane, *B.M.*, and bearing several very long cilia, *Cl.*, on the distal surface. The cilia are about as long as the cell, and are inserted on a basal knob. The nucleus is rather elongate, and is situated near the base of the cell. The cell contents are of a variable nature; usually the cell is filled with a finely granular pink-staining substance, hæmatoxylin-eosin stain, in which are numerous spherical masses that stain a dark red. Other cells present a vacuolated appearance, as if filled with a foamy fluid substance. Since the function of these cells is absorption, the different appearance of the contents should correspond to the different stages in the absorptive process. Throughout the greater part of the middle intestine the cells are swollen with the food contents, and so closely pressed together that it is impossible to make out the details of a single cell. All cell walls have apparently disappeared, and the result is a chaotic mass of cytoplasm filled with globules and granules of food, bordered by cilia on the side toward the intestinal lumen, and with a row of nuclei along the base, above the basement membrane.

The gland cells that have been mentioned as occurring occasionally in the middle intestine, fig. 34, *Gl.*, cannot be distinguished from the absorptive cells—except by their absence of cilia—in preparations stained with iron-hæmatoxylin, since with this stain both the secretion globules and the absorptive particles stain black. With the hæmatoxylin-eosin stain, however, the differences are strongly brought out, the food granules staining a brighter red, and having a different degree of refraction from that of the glandular secretion globules.

It has already been mentioned that the two anterior pouches consist of different histological elements from the subsequent ones. They are also somewhat smaller and are deflected slightly forward (see fig. 1). In the more anterior part of the middle intestine, the cæca are but little deeper than the axial part of the canal, but farther back the cæca increase in depth at the expense of the axial portion.

In the breeding season, when the gonads are swollen and enlarged, the intestinal cæca are under such pressure that their opposite walls are frequently in contact. Wilson (1900) believes that the lateral cæca do not function under these conditions, and quotes the statement of M'Intosh (1873), that "the glandular elements in the wall of the digestive tract undergo a certain amount of atrophy during the period of reproductive perfection." Wilson adds, in respect to *Cerebratulus lacteus*, p. 115: "For a long time, therefore, these intestinal pouches can function very little, if at all, and so they contribute nothing to the nourishment of the body." I should be unwilling to state that the lateral pouches in *Zygeupolia* take no part in the absorption of food, for I have found some cells of the lateral cæca that evidently contained food vacuoles, in spite of the fact that the cæcum was greatly pressed by the adjoining gonads; but the cells of the cæca are certainly under great disadvantages at this period.

Toward the posterior end of the body (see fig. 17), the lateral cæca decrease more and more in size, until finally the intestine is once more a simple tube, Plate XLI, fig. 26, *E.I.* This portion of the alimentary tract is variously termed the "anal portion of the intestine," the "end intestine" ("Enddarm," Bürger) and the "rectum" (Coe, 1895 *a*).

The end intestine, as it will here be termed, in *Zygeupolia* is about .8 mm. long. The cells are the same absorptive cells that are found in the middle intestine, with an occasional gland cell, so that histologically the end intestine is the same as the middle intestine, and may be regarded as merely the terminal portion of that region.

At the junction of the caudicle and body, fig. 27, the intestine curves dorsally and opens, by the anus, to the exterior on the dorsal surface of the body. The anal opening, fig. 17, *A.*, is small, and the edges are clothed with cilia.

10. THE REPRODUCTIVE SYSTEM. — *Zygeupolia* is dioecious. The gonads, figs. 1, 24, 25, are found between the pouches of the middle intestine, metamerically arranged, throughout its length, the first pair of gonads occurring between the first and second pairs of intestinal cæca, and so on regularly, the gonad of one side lying between two consecutive intestinal cæca, and opposite to its fellow of the other side. Near the end of the middle

intestine, about 7 mm. anterior to the anus (see fig. 17), where the cæca become more and more shallow and finally disappear altogether, leaving the simple tube of the end intestine, the gonads terminate (cf. fig. 26).

The Testis.—The testis is a simple sac, the wall consisting of a one-celled layer of large, rather flattened cells with prominent nuclei. In cross section, Plate XLI, fig. 24, the wall of the gonad appears like a membrane, along which the nuclei are placed; in tangential section, Plate XLIII, fig. 53, the cells appear elongated, dovetailing into one another, with strong cell walls which are wavy in outline, and granular cytoplasm that stains pink with the hæmatoxylin-cosin stain. Each testis has a single duct, figs. 24, 55, *T.d.*, opening on the dorsal surface of the body, very near the side of the rhynchocoel. The duct passes dorsally from the testis through the inner longitudinal and circular muscle layers, and then expands into a bulb-like portion with slightly thickened walls, fig. 55, *b*, and again narrows before opening to the exterior. The duct meets the body epithelium at the surface, and no bending in of the latter has been observed.

The youngest male cells are found at the margin of the testis, attached by their bases to the gonad walls, figs. 24, 57. The youngest cells are the largest—.023 mm. long, .005 mm. wide. They are rather pear-shaped cells, fig. 57, with the distal end rounded and the basal end prolonged into a slender stalk. The nuclei, *N.*, are large, with a prominent chromatin reticulum and one nucleolus, *n.* The cytoplasm is finely granular and no cell membranes are present. From their size it is probable that these cells are spermatogonia. They form a layer, one or two deep, around the periphery of the testis, and are occasionally found far in toward the middle.

On the median side of the spermatogonia comes a zone of smaller cells, arranged in radial rows. These are probably spermatocytes. Many of them are in division stages, and the tiny spindles are very distinct, but are too minute for any exact study.

In the innermost part of the testis the spermatozoa, Plate XLI, fig. 24, *Spz.*, are found, and near them very small cells that are no doubt the spermatids. The spermatozoa are about .06 mm. long, and three parts may be distinguished in them, the head, the middle piece and the tail, Plate XLIII, figs. 58, 59. The head is longer

than wide, and is slightly broader at its posterior end. It stains deep black with iron-hæmatoxylin, and blue with hæmatoxylin-eosin. In some iron-hæmatoxylin preparations that had been strongly destained, the head appeared ashy gray with a minute black point at the tip, fig. 58. The middle piece, *m.b.*, is a four-lobed structure. In fig. 59 there is a middle piece that has been detached from a spermatozoan and which resembles four small spheres. In side view only two of the lobes are seen. The middle piece stains black with iron-hæmatoxylin, and red with hæmatoxylin-eosin. The tail is a slender filament, in which no structure could be made out, many times longer than the head.

The Ovary.—The wall of the ovary, like that of the testis, is a flattened epithelium, fig. 54, *Gon. W.*

No ovarian duct has been found, although several specimens of different ages have been examined. It is possible that a duct may form in an older stage than those studied, but it seems more probable that the eggs are discharged by rupture of the wall. The latter view is supported by the fact of the difficulty in keeping the body wall intact while studying living females with large ova. When a perfect specimen was placed on a slide with sea water and covered, a method that was repeatedly used without difficulty for males, and for females with smaller ova, the posterior part of the body would almost invariably fragment. It was also difficult to fix and harden a mature female without rupturing the body wall. No especial importance was attached to these facts at the time, but since finding from the study of sections that there is no preformed ovarian duct, I am inclined to believe that the fragmentation observed in the female specimens was caused by the rupture of the body wall above the gonads, the break then extending farther around the body wall.

Closely pressed against the wall of the ovary and attached to it by their broad bases are the youngest egg cells.¹⁰ Fig. 54 is a cross section of a portion of the wall of one of the youngest ovaries. Although most of the smallest ova are distinct cells, here and there several are seen, so close together that their boundaries cannot be distinguished, and it is therefore probable that the ova arise from a

¹⁰ As all the material examined was quite advanced in age, I have had no opportunity to study the youngest stages of the ova, so that therefore the cells that are here described as the youngest are probably well on in their development.

cell syncytium. The smallest separate egg cells, *O.*₁, are rather square, having as yet no stalk. The cytoplasm is clear and slightly granular, with no yolk granules, and there is a delicate cell membrane. The nucleus is round, about .0058 mm. in diameter; a small nucleolus is present, but no chromatin is demonstrable, probably on account of admixture with plastin, and the whole nucleus takes a plasma stain, pink with hæmatoxylin-eosin.

In the next stage, the young ovum, *O.*₂, has lengthened, the distal end is somewhat rounded and the proximal end more slender, so that the whole cell is now pear-shaped. The proximal end constricts more and more until it becomes a slender stalk, by which the rounded distal end or cell body remains attached to the gonad wall. The nucleus has enlarged, measuring about .023 mm. in diameter, likewise the nucleolus, in which scattered vacuoles are forming. Yolk granules are beginning to appear in the cytoplasm.

After the appearance of the yolk the cytoplasm has quite a different look, being denser with the fine yolk granules scattered throughout. The nucleus of this stage, *O.*₃, is much larger, .035 mm. The nucleolus has not increased much in size, but the small scattered vacuoles have fused into one large disk-shaped vacuole, *n.vac.*, at the periphery of the nucleolus.

The ovum is now surrounded by two egg membranes, the outer of which, *o.O.mb.*, is considerably thicker than the inner and stains blue, while the inner takes a faint pink, hæmatoxylin-eosin stain. The formation of the egg membranes has not been followed with any exactness, but I believe that both membranes are formed by the egg. Böhmig (1898) believes this is the case in *Stichostemma gracense*. Montgomery (1895) states that in *S. eilhardi* only the inner egg membrane is a "yolk membrane," the outer being derived from the germinal epithelium and is therefore a true chorion.

The oldest stage found, figs. 25, 52, is that of a free ovum in the centre of the gonad, no longer attached to the wall by its stalk. Both membranes are present, the outer one, fig. 52, *o.O.mb.*, being often broken and discontinuous, as if it were about to be sloughed off. This appearance, however, may be an artifact, as the specimen from which it is drawn was badly shrunken. At this stage the gonad contains twenty or more ova of equal size, in such close contact with each other that they assume a polygonal

form. This is seen in fig. 56, a slightly younger stage, drawn from life. It is likely that several or many ova ripen in one gonad at once, and not one at a time as in many Nemerteans.

The cytoplasm of this oldest stage stains a bright pink with the hæmatoxylin-eosin stain, and is charged with yolk; the nucleus is very large, its diameter being about half that of the cell, the greater part of its contents still taking the plasma stain. The nucleolus is either one large rounded body, usually placed peripherally, or it is broken up into numerous small fragments, which lie around the periphery near the nuclear membrane, fig. 61, *n*. Several vacuoles of varying size are present in the nucleolus.

The attempt has been made to determine whether there is any priority in the ripening of the sexual products of either end of the body. No difference in the respective ages of the gonads of the two ends has been observed in the specimens studied. In any one immature gonad different stages may be found, the youngest cells lying peripherally, attached to the gonad wall, the older cells toward the centre and free.

11. THE CAUDICLE.—The caudicle, a term suggested by Montgomery (1897 *a*) as a translation of Bürger's "Schwänzchen," may be defined as the slender, thread-like process at the posterior end of the body of certain Heteronemerteans.¹¹

The caudicle of *Zygeupolia* in life, figs. 4, 5, 6, appears as a slender white filament, and a low magnification reveals a ciliated surface and what seems to be a quite regular segmentation. A closer examination, however, shows that the apparent annular constrictions are merely the result of muscular contractions, and are constantly varying in size and position. A light area along the mid-line, bordered by denser areas, indicates the presence of a central cavity—the blood lacuna.

In connection with the caudicle, a description of the position of the organs in the extreme posterior end of the body may be of interest. The division of the dorsal blood vessel into two has already been mentioned, and the subsequent fusion of the four vessels into a central blood space; the termination of the rhynchocœl; the disappearance of the gonads and the dorsal opening of the anus. A short distance in front of the anus the lateral nerves

¹¹ It will be shown in the historical review of the literature of the caudicle, that the structure described as a caudicle by Montgomery (1897 *a*) is in reality a regenerating posterior end.

assume a more ventral position, finally lying on the ventral surface of the body, Plate XLI, fig. 27. In this position they pass over into the caudicle. In the caudicle, fig. 28, *C.L.N.*, the nerves lie latero-ventrally, and extend to the posterior end.

The transition from the end of the body to the caudicle is also marked by the sudden disappearance of the cutis and outer longitudinal muscle layer. This is seen in fig. 27, a slightly oblique cross section, that passes through the wall of the body dorsally and the wall of the caudicle ventrally.

A cross section through the caudicle, fig. 28, shows that it is a hollow tube with the following structure: (1) the epithelium, (2) the two lateral nerves in the epithelium, (3) the circular muscle, (4) the inner longitudinal muscle, and (5) mesenchyme cells bordering on the central blood space.

The epithelium is composed of ciliated supporting cells, fig. 12, *S.C.*, very similar to those of the body, but with a smaller cell body and longer stalk (cf. figs. 2 and 12); large gland cells, fig. 11, lying mostly on the dorsal surface, the secretion staining red with eosin, with very large nuclei at the base and abundant cytoplasm enclosing the secretion; and very numerous interstitial connective tissue cells between the bases of the epithelial cells, above the basement membrane. The epithelium of the caudicle as a whole is slightly higher than that of the body, measuring about .04 mm. in height. The nuclei of the connective tissue cells, fig. 28, *Cn.T.N.*, are so prominent and the cells so numerous that the effect is like that of undifferentiated tissue. Bürger¹² (1895), p. 239, says in this connection: "Es lässt der Reichthum an Kernen wohl keinen anderen Schluss zu, als dass die Zellelemente der Gewebsschichten und des Parenchyms des Schwänzchens im Vergleich zu denen des Körpers ganz ausserordentlich klein sind."

The lateral nerves, fig. 28, *C.L.N.*, lie in the epithelium outside the circular muscle layer, latero-ventral in position. No ganglion cells could be detected around the fibrous core. The circular muscle layer, *C.M.*, is reduced to a very thin layer of two or three fibres; the longitudinal muscle, *i.L.M.*, is also a layer of but little thickness. The central blood space, *Bl.L.*, is bordered by scattered mesenchyme cells, *mes.*, large pear-shaped cells, attached at first to the muscular wall, but later floating freely in the lacuna.

¹² For the sake of clearness the great numbers of the connective tissue cells in the epidermis are not represented in fig. 28.

It is thus seen that the caudicle of *Zygeupolia* is a structure from which many organs of the body are absent, namely: the alimentary canal, the gonads, the rhynchocoel, the outer longitudinal muscle layer and the cutis.

The significance of the caudicle, however, is not clear, and several explanations may be suggested: (1) The caudicle has remained in a simple, primitive or embryonic condition, while the rest of the body has become differentiated.

(2) The caudicle is a degenerate structure, the degeneration of certain organs having begun at the posterior end and continued gradually forward.

(3) The caudicle is a cœnogenetic structure, with a certain physiological function.

Of these views, no positive proof can be brought forward in regard to the first two. The varying complexity of the caudicles of different genera—for example, that of *Zygeupolia* and the caudicle described by Bürger (1895) for *Cerebratulus marginatus*, containing all the organs of the posterior end of the body—might support the view of degeneracy, but this argument may hardly be used until we know more of the origin and phylogeny of the caudicle.

It seems much more probable that the caudicle of the Nemerteans has arisen cœnogenetically, and an explanation of its mode of origin has been suggested by the comparison with a Rhabdocœl Turbellarian, *Macrostoma hystric* Oe., described by Graff (1882), and figured on Taf. IV, Fig. 1. In this worm the posterior end is expanded laterally and provided with abundant gland cells, making an adhesive surface. Graff says, p. 240, the body is “hinten in einen platten spatelförmig erweiterten Schwanz ausgezogen.” It would not be difficult to imagine this posterior end becoming elongated and more slender, until it is finally a thin filament. In a similar way the Nemertean caudicle may have arisen from a posterior end, originally differentiated as an adhesive surface. The observations of Johannes Müller (1854) and M’Intosh (1869) show that at the present time the end of the caudicle frequently acts as a sucker.

M’Intosh (1869) believes that the central space in the caudicle of *Micrura purpurea* is connected with the circulatory system. This, as stated above, is certainly true in *Zygeupolia*. The fact

that the large blood lacuna occupies the entire space within the muscular wall of the caudicle of *Zygocypolia*, and that the mesenchym—blood-forming—cells are very abundant, suggests that one function of the caudicle may be the formation of new blood cells. This, however, also takes place throughout the blood vessels of the body. The large blood lacuna of the caudicle is probably a means of aerating the blood, making respiration another possible function of this problematical structure.

Literature of the Caudicle.—The caudicle has been known in literature under various other names, and considerable confusion has arisen from the multiplication of terms, and from the fact that the caudicle, which is an adult structure, has been confounded with the regenerating “papilla” so frequently found at the posterior end of Nemerteans that have been broken.

For this reason an account of the history and synonymy of the caudicle and the differences between the true caudicle and the regenerating posterior end will be given, at perhaps greater length than the importance of this small structure demands.

The following papers will be separated under two headings I, those describing the true caudicle; II, those in which other structures have been mistaken for the true caudicle.¹³

I. Ehrenberg and Hemprich (1831) describe the new genus *Micrura* with “anus sub cauda,” and *Micrura fasciolata* nov. sp., “. . . . anus terminalis sub processu caudali parvo, albo.”

Busch (1851) (cited by J. Müller, 1854) mentions and figures, Taf. II, Fig. 8, a Nemertean with a caudicle (“Schwanzanhang”). The worm is described under the name of *Alardus caudatus*.

Diesing (1851) refers to *Micrura* Hemp. et Ehr. = *Nemertes* Oersted, as with a “processu terminali postico filiformi brevissimo.” He describes the new species *Meckelia Knerii* Diesing, “corpus depressum retrorsum parum augustatum processu brevissimo filiformi.”

Dalyell (1853), Vol. II, (cited by Krohn, 1858), describes under the name *Gordius* four Nemerteans that would now be

¹³ In this review of the history of the caudicle some of the earliest and some of the most important papers in Nemertean literature are referred to, but no attempt has been made to give a complete list of all the observations on the subject.

recognized as *Micrura*. They are *G. viridis spinifer*, *G. purpureus spinifer*, *G. fragilis spinifer* and *G. fasciatus spinifer*.

Johannes Müller (1854) reports finding a young worm within the larva *Pilidium gyraus*, and also others in the water which have a "Schwanzanhang," and resemble the *Alardus caudatus* Busch. The latter is figured, after Busch, on Taf. IV, Fig. 2. Müller says "Mit dem Schwanzanhang kann sich das Thierchen auf dem Glase anhalten und wie festleimen und ist dann schwer von der Stelle zu bringen." He believes that the young worm within the larva, resembling the *Alardus* of Busch, is the same as *Micrura fasciolata* Ehr. et Hemp. Müller also quotes a letter from A. Krohn, dated November 19, 1851, in which Krohn speaks of finding at Naples a young worm within the *Pilidium gyraus*: "Der Leib desselben ist länglich oval, nach vorn zu etwas verschmächtigt. Mitten am hinteren Ende findet sich ein ganz kurzer cylindrischer Anhang, der durch wenige aufeinander folgende Querschwülste wie gegliedert erscheint. Die Oberfläche des Leibes, so wie auch die des Anhanges ist wie bei den Turbellarien dicht mit schwingenden Cilien besetzt."

Krohn (1858), referring to the young worm within the *Pilidium gyraus*, says: "In Helgoland sah ich 1854 mehrere arten von *Pilidium*. . . . Der Schwanzanhang wird an den meisten Nemertinen von Pilidien beobachtet, und wird nur selten vermisst. . . . Die Nemertinen mit Schwanzanhang gehören zu der Gattung *Micrura* Ehr., womit *Alardus* Busch identisch ist." On p. 300, Krohn gives a list of the *Micrura* found in the North Sea, and an account of the synonymy of the genus.

Leuckart (1858) summarizes the work done on Nemerteans. On p. 186 he mentions the "Anwesenheit eines retractilen Schwanzfadens" in a Nemertean.

Leuckart and Pagenstecher (1858) describe a new *Pilidium*, *P. auriculatum*: "Ein Schwanzfortsatz, wie er so häufig bei den in Pilidien gebildeten Nemertinen gefunden wird und nach J. Müller auch bei dem Sprösslinge eines Helgoländer *Pilidium* vorkommt, fehlt unserm Thier."

Metschnikoff (1869) mentions the presence of a caudicle on the young worm within the pilidium. This is figured on Taf. X, Fig. 15. On p. 55 he says: "Es bildet sich am Hinterrande der jungen Nemertine ein kleines konisches Schwänzchen, welches

einen einfachen Auswuchs der Körperwand darstellt, und wie diese mit Flimmerhaaren bedeckt erscheint."

M'Intosh (1869) describes the following structure: "The posterior end of the body in *Micrura* (*Stylus*) requires special mention, since there is superadded a peculiar elongated and contractile style. This appendage seems to be formed by a prolongation of the cutaneous and part of the muscular (longitudinal and circular) textures of the body wall of the animal. The entire organ in contraction has a granular appearance, the coarsest granules and occasionally a few circular masses of brownish pigment, being at the tip. Within these coats is a circular chamber, which undergoes various alterations in size, and contains a transparent fluid. This cavity is not connected with the digestive tract, which opens by a terminal pore at the base of the process, nor can proboscidian discs be seen therein. . . . its connection with the circulatory [system] appears most probable."

M'Intosh (1874) says that the genus *Micrura* has "a soft filiform caudal process, capable of attachment." He further alludes to "a pale caudal filament" and "a slender styliform process attached to the tail" which "can be elongated to an extreme degree."

Hubrecht (1887) used the term "caudal papilla" throughout his description of the caudicle.

Verrill (1893), in defining the genus *Micrura*, says: "Posterior end of the body provided with a median slender cirrus, above the anus. This genus, as here defined, differs from *Lineus* in little else than the presence of a well-marked contractile anal cirrus, which may often be distinguished even in alcoholic specimens. From *Cerebratulus*, which also has the anal cirrus, it differs in the form and muscular structure of the body posteriorly." In other parts of this work the terms "anal papilla," "caudal papilla" and "caudal filament" are indiscriminately used.

Verrill (1895) employs the expression "caudal cirrus."

Bürger (1895) describes "ein dünnes 5-15 mm. langes, meist borstenartig starres, weissliches Anhängsel," which he terms "das Schwänzchen." On p. 24, in reviewing the work of Dalyell, Bürger employs another term, saying that Dalyell "den Appendix beobachtet und gut gezeichnet hat."

Coe (1895 *a*), in regard to *Cerebratulus lacteus*, says: "The anus is at the end of the body, just beneath the caudal papilla."

Coe (1901) gives as one of the generic characters of *Cerebratulus*, ". . . the posterior end extremely flattened and provided with a delicate caudal cirrus, which extends beyond the opening of the intestine."

Wilson C.B. (1900) uses Hubrecht's term "anal papilla" for the caudicle of *Cerebratulus lacteus*.

Punnett (1900) speaks of a "caudal appendage."

II. O. F. Müller (1788) describes and figures, p. 38, tab. 68, figs. 18, 20, a *Planaria filaris*: "*Planaria linearis cauda filiformi contractili*." The length of the "cauda filiformis contractilis" in fig. 20, equal to the length of the body, suggests the thought that it may be the evaginated proboscis. Bürger (1895), p. 8, says that this worm is probably a *Tetrastemma*.

Grube (1855) describes two new species of *Meekelia*. The first, *M. annulata*, resembles the *M. Knerii* Diesing. Grube thinks that the "processus terminalis" described by Diesing is more probably a regenerating end; he says: "Der processus brevissimus filiformis könnte ein reproducirtes noch junges Schwanzende sein." The second species, *M. aurantiaca*, has the following characteristics: "Der Körper verschmälert sich nach hinten sehr allmählich, und endete bei einem Exemplare in ein viel dünneres, wahrscheinlich vor kurzem reproducirtes Schwänzchen."

Montgomery (1897 *a*), Taf. 2, Fig. 16, has described as a caudicle what is evidently a regenerating posterior end.¹⁴ The characters that make the structure described by Dr. Montgomery in *Cerebratulus lacteus*, and figured by him on Taf. 2, Fig. 16, a regenerating posterior end rather than a true caudicle are (1) the size, (2) the presence of the alimentary canal, (3) the presence of the outer longitudinal muscle layer, and (4) the presence of the three distinct blood vessels with definite walls.

The chief external differences between the true caudicle and the regenerating papilla of *Cerebratulus lacteus* are in size and general

¹⁴ My attention was called to this error by Dr. Montgomery himself, who has suggested that it be rectified. Dr. Montgomery has kindly lent me his own preparations upon which the observations were made, so that I have been able to compare them with slides of my own, made from a *Cerebratulus lacteus* found in life with a good-sized regenerating papilla, which bore a short caudicle at its posterior end.

appearance. The true caudicle is slender and thread-like, contractile and usually twisted; the regenerating papilla is stouter and rod-like, and does not twist and contract like the caudicle. C. B. Wilson (1900) contrasts the two structures as follows. On p. 116, alluding to the regenerating end, he says: "Such a papilla is slender and almost pure white in colour. At first it is difficult to distinguish it from the true anal papilla with which the body normally terminates, but it may be recognized by the fact that it always possesses a very broad base which fades gradually into the body wall, while the anal papilla is narrow and ends abruptly at the emargination."

The papilla on the *Cerebratulus* found by the writer was about 7 mm. long, light in color and rather rounded, not yet having assumed the typical flattened shape of the body. At its posterior end a short, but in all respects a true caudicle was borne. A cross section through this true caudicle shows that it consists merely of a thin body wall enclosing a central blood space. The body wall is composed of the epidermis, in which the two lateral nerves lie, and of the circular and inner longitudinal muscle layers. The blood lacuna has no definite lining, but is bordered by numerous mesenchym cells. From the caudicle of *Cerebratulus lacteus*, like that of *Zygeupolia*, the alimentary canal, the gonads and the rhynchocoel are absent.

A cross section through the regenerating papilla of my *Cerebratulus* has the same structure that is found in the section figured by Dr. Montgomery. The outer longitudinal muscle layer and the alimentary canal are present, and three blood vessels—one dorsal and two lateral—instead of the central blood lacuna. This proves finally that the structure observed by Dr. Montgomery is a regenerating posterior end and not a caudicle.

In both worms the end of the body tapers quite gradually into the regenerating portion, and it would be difficult to say where the old tissue ends and the new begins, as differentiation has evidently gone on for some time in the anterior part of the new tissue. The most posterior sections of Dr. Montgomery's worm show that a true caudicle had likewise begun to form there, but had subsequently been broken off just at its base. It is seen from the measurements of the two worms that there is an abrupt change in size between the end of the body proper and the caudicle, the caudicle

measuring less than half the width of the body. The diminution in size is due to the sudden disappearance of the outer longitudinal muscle layer, and to the ending of the alimentary canal with the body.

A word must be said here in regard to the relative position of the anus and the caudicle.

Verrill (1893) states that the caudicle of the genus *Micrura* is above the anus, and Coe (1895) says the same in regard to *Cerebratulus lacteus*. From my study of sections of *Micrura caeca* and *Cerebratulus lacteus* I find that the anus undoubtedly opens dorsally *above the caudicle*. Nothing is easier than to confuse the dorsal and ventral surfaces of a living worm, but in serial sections, with definite structures for orientation, there can be no such difficulty. The anus in *Zygeupolia* likewise opens dorsally *above the caudicle*, and Bürger (1895) states that the dorsal position of the anus is usual in Nemerteans. From these data it seems likely that a thorough investigation of all species with caudicles will prove that the dorsal position of the anus is of general occurrence.

Bürger (1895), p. 238, says in regard to the caudicle of *Cerebratulus*, *Micrura* and *Langia*: "Morphologisch stellt das Schwänzchen nichts anderes dar als das stark und meist plötzlich verjüngte hintere Körperende, in das sich von Organen der Darmtractus, die drei Blutgefäßsstämme, die Genitaltaschen und die Seitenstämme fortsetzten, und in welchem wir auch alle Schichten der Körperwand bis auf die Cutis, welche gänzlich verschwunden oder in ihrer Ausbildung fast unterdrückt ist, antreffen." According to this all the organs of the posterior part of the body are represented in the "Schwänzchen," except the rhynchocœl, and even this organ, Bürger states, is present in the anterior part of the caudicle of *Cerebratulus marginatus*.

The observations of M'Intosh (1869) in regard to *Micrura purpurea*, those of Verrill (1893) on the whole genus *Micrura*, and my own upon *M. caeca* are contradictory to the above statement of Bürger. In like manner Coe's work upon the American species of *Cerebratulus* and my own upon the one species *Cerebratulus lacteus* show that the caudicles of these forms cannot be regarded as merely "verjüngte hintere Körperenden." From the very limited space devoted to the subject of the caudicle in Bürger's great monograph, it is likely that his study of this structure was

hasty, and the question has arisen in my mind, could Bürger have mistaken a regenerating posterior end for a true caudicle?

Without wishing to criticise the statement of this distinguished investigator, it seems probable that a further investigation of the caudicles of the European species of *Micrura* and *Cerebratulus* will result in an agreement with the structure of the American species.

III. PARASITES.

A monocystid Gregarine in its adult form is frequently present in the middle intestine of *Zygeupolia*. Large cysts, surrounded by a thick cuticle and containing various developing stages, are also found in the intestine. From their proximity to the adult Gregarines, and from their resemblance to the stages figured by different authors, it seems likely that these are Gregarine cysts. Outside of the cyst, in the lumen of the intestine, are small amoeboid masses, resembling some of the stages within the cyst. These amoeboid masses also penetrate between or into the cells of the intestinal wall and probably into the gonads.

In some living specimens large white spots may be noticed among the gonads, fig. 6. They are so large that they are easily seen with the unaided eye. They appear stalked, like the ova, and have a large nucleus with one or more nucleoli. Fig. 56, a horizontal optical section drawn from life, shows one of these structures in a gonad together with several ova. In life the cytoplasm appears denser and darker than that of the small ova, and the conclusion first reached after studying these living bodies was that they were the oldest, nearly mature ova.

The examination of sections in which these large bodies are present has shown that the first conclusion was erroneous and has proved that they are the encysted stages of some parasites within the cytoplasm of the ovum. Fig. 60 is a transverse section through the body wall and the wall of the gonad, showing the cyst, surrounded by egg cytoplasm, *ey.*, and attached to the gonad wall, *Gon. W.* The cyst is surrounded by a striated cuticle,¹⁵ *Ctl.*, and outside the cuticle is a delicate membrane staining like the cell membrane. In the cytoplasm of the base are two egg

¹⁵ The reference line from *Ctl.*, fig. 60, only extends as far as the egg membrane, instead of to the cuticle within.

nuclei, *N.* The cytoplasm of the cyst has a very different staining reaction from that of the egg, staining a faint violet with hæmatoxylin-eosin, and having a finely granular appearance. The nucleus of the cyst, *N.par.*, is irregular in outline, in some specimens with amœboid processes. It stains homogeneously a bright red, hæmatoxylin-eosin, while the nucleoli are darker and frequently vacuolated.

The presence of the additional egg nuclei in the cytoplasm at the base of the cyst render it probable that the parasite entered the cytoplasm when the ovum was in a syncytium. The presence of the parasite may have caused an abnormal growth of the egg cytoplasm, or the latter may have merely expanded with the growth of the cyst. In its appearance the cytoplasm around the cyst is like that of the normal, uninfected eggs.

Figs. 48, 61, show two infected egg cells from a different individual, with amœboid, probably earlier stages of the parasite, *Par.* In this particular worm almost every egg has been infected.

As a rule, the gonads of the male specimens that were studied were not infected, but in a few worms the testes contained large bodies that were evidently parasites, and that resembled some of the stages found in the ovaries.

The relation, if any exists, between the amœboid masses found in the intestine and those within the egg cells has not as yet been worked out, as it is not within the scope of the present paper, but in consideration of the prominence of these parasites and of their position in the ova, this brief description has been given. If sufficient material can be obtained for the intermediate stages, this subject may later be studied in detail.

The presence of adult Gregarines in Nemerteans has been known for a long time, and they are mentioned and described by several of the earlier Nemertean writers—Frey and Leuckart (1847), Kölliker (1848) and Johnston (1865), Appendix, p. 290.

I have found no references in literature to any structures quite similar to those found in the ova of *Zygeupolia*. M'Intosh (1867) and Wheeler (1896) describe parasites that have a certain degree of likeness.

M'Intosh found adult Gregarines in *Borlasia octoculata* = *Lineus sanguineus* and *Borlasia olivacea* = *Lineus gesserensis*. Besides the adult Gregarines, M'Intosh found what he called "certain

ova that accompany the Gregarines." The "ova" measured about $\frac{1}{400}$ inch in diameter and each contained an "embryo" that made evident movements. They have two coats, an inner faintly striated and an external without markings. The contained "embryo" is finely granular and has a large pale nucleus. M'Intosh regards these "ova" as altogether different from the true ova of the *Borlasia*.

Wheeler found in the body cavity of the Annelid *Myzostoma glabrum* great numbers of amœboid masses that he regards as possibly the young stages of some Gregarine. The body cavity was distended with ova, and among them occurred the parasites. He says: "In most cases the uniformly staining and rather shrunken body of the parasite was produced into a long fine point which had penetrated the cytoplasm of an ovum. In a few instances a single amœba had two points, each entering the body of an adjacent ovum (fig. 54). The cytoplasm of the ova thus attached contained large granules which took up the hæmatoxylin with avidity. These granules were larger and more numerous than those which occur in normal ova of about the same size." The amœbæ are also found outside the ova.

IV. GENERAL CONCLUSIONS.

The description of the organs of *Zygeupolia* given in the anatomical section of this paper makes it evident that this genus is a primitive one and that it has affinities with both Proto- and Heteronemerteans.

The questions now to be discussed are (1) the relationship of *Zygeupolia* to other orders, especially the Protonemerteans; (2) the position of *Zygeupolia* within its own order.

The following characters undoubtedly entitle *Zygeupolia* to a place in the order of the Heteronemerteans: the position of the lateral nerves, outside the circular muscle layer; the presence of the cutis and outer longitudinal muscle layer; the situation of the mouth behind the brain; the absence of stilets in the proboscis and of a blind intestine.

The alimentary system of *Zygeupolia* conforms with the general Heteronemertean plan, which, however, is essentially the same as that of the Mesonemerteans and such Protonemerteans as *Carinina* and *Hubrechtia*.

The blood system of *Zygeupolia* is of the Heteronemertean type, *Hubrechtia* being the only Protonemertean that approaches it in any way, namely, in the presence of a dorsal blood vessel.

In the structure of the nervous system and the cerebral sense organs *Zygeupolia* is again a Heteronemertean; but by no means the highest type of brain or sense organ is represented, *Zygeupolia* having a very simple Heteronemertean brain and cerebral sense organ.

The presence of muscular crosses in the proboscis and its general structure are further characters in common with certain Heteronemerteans.

The absence of lateral slits is a primitive character, and one common to all the Protonemerteans and to the more primitive Heteronemerteans. This character, as we know, is possessed by *Zygeupolia*. The inner circular muscle layer of *Zygeupolia* is, in my belief, a primitive character, and the short extent of the layer is explicable on the grounds that the thickened region in front of the middle intestine is only the remnant of a layer that was once continuous throughout the body.

The presence of this muscle layer in a limited region in *Micrura cæca*, and of a similar layer in *M. alaskensis*, Coe (1901), shows that an inner circular muscle layer exists in two genera of the Heteronemerteans. The dorso-ventral fibres of the Heteronemerteans, regarded by Bürger as derived from an inner circular layer, and the so-called "oesophageal muscles" ("Darmmuskulatur") which, according to my view, are derived from the deflection and bending around of dorso-ventral fibres, are other evidences of the remains of an inner circular muscle among the Heteronemerteans.

The lateral grooves of *Zygeupolia*, if they are sense organs, may possibly be homologized with the side organs of *Carinella*. Their position in the median lateral line of the body, and their character as epithelial grooves, both agree with the side organs; but until their undoubted sensory character is proved, the comparison should not be emphasized.

A brief summary of the structure of *Zygeupolia* shows that it is a Heteronemertean, on account of the presence of the outer longitudinal muscle layer, the position of the lateral nerves, the structure of the alimentary system, of the blood system, of the nervous

system and cerebral sense organs, and of the proboscis; while the affinities with the Protonemerteans—and certain Heteronemerteans—are in the absence of lateral slits, in the presence of an inner circular muscle layer and of crosses between this layer and the outer circular, and in the lateral grooves, if sense organs.

The general simplicity of its Heteronemertean structure and the several Protonemertean characters bring *Zygeupolia* very near to the Protonemerteans, and through *Zygeupolia* the whole Heteronemertean order is more closely connected with the Protonemerteans.

The question now arises, To which of the families of the Heteronemerteans does *Zygeupolia* belong—to the Eupoliidæ, or to the Lineidæ?¹⁶

The chief characteristics of the two families will now be given, according to Bürger (1895):

The Eupoliidæ.—(1) No lateral slits in the head, the cerebral canal opening directly outward or into shallow ventral furrows.

(2) No muscular crosses in the proboscis.

(3) The proboscis musculature consists of two layers, an outer circular and an inner longitudinal muscle layer.

(4) A head gland is prominent, the gland cells reaching back into the œsophageal region.

The Lineidæ.—(1) The canal of the cerebral organ opens usually, not directly outward, but into deep, or sometimes shallow, lateral slits in the head.¹⁷

(2) Two muscular crosses in the proboscis.

(3) The proboscis musculatur consists of three layers—longitudinal, circular and longitudinal muscle layers; if any one of these layers is absent it is the inner longitudinal one.

(4) The head gland is represented by a few gland cells, and does not extend posterior to the brain.

¹⁶ In my preliminary note upon *Zygeupolia* (1900 a) this genus is placed in the Eupoliidæ, on account of the absence of lateral slits and the supposed absence of muscular crosses in the proboscis. As I have since found muscular crosses in the proboscis, I wish to correct this error.

¹⁷ Bürger's own words in regard to the lateral slits are here given (1895, p. 613): "Der Canal des Cerebralorgans mündet in der Regel nicht direct nach aussen, sondern in tiefe laterale horizontale Taschen, welche durch die Kopfspalten gebildet sind. Die Kopfspalten sind wechselnd tief: sie schneiden häufig bis auf das Hirn ein, aber sie sind auch, obwohl in seltenen Fällen, nur durch flache laterale Längsbuchten angedeutet."

The Lineidæ are subdivided into the Amicruræ, forms without a caudicle, and the Micruræ, forms with a caudicle.

Zygeupolia agrees with the above description of the Eupoliidæ in one point only, *i.e.*, in the absence of lateral slits in the head. The number of the muscle layers of the proboscis is the same in both, but the position of the layers is reversed in *Zygeupolia*, the longitudinal muscle being the outer; the circular, when present, the inner. It will be recalled that the circular layer is absent from the "anterior region" of the proboscis of *Zygeupolia*.

The structure of the proboscis musculature of the "middle region" in *Zygeupolia* agrees with what Bürger evidently regards as the less common condition in the Lineidæ, namely, in the absence of the innermost of the three muscle layers.

Muscular crosses are found in the proboscis of *Zygeupolia*; but this is a very variable character, for different individuals may have a dorsal and ventral cross of equal size, a strong dorsal with a faint ventral cross, or a dorsal cross only.

The absence of a definite head gland and the presence of a caudicle are common to both *Zygeupolia* and the Micruran Lineidæ.

The neurochord cells of *Zygeupolia* are an evidence of specialization, for hitherto these cells have been found only in highly organized genera.

It is evident that *Zygeupolia* agrees best with the exceptional members of the Lineidæ—*i.e.*, with those Lineidæ whose cerebral canals open directly to the exterior, and from whose probosces the inner longitudinal muscle layer is absent.

When we therefore consider the position of *Zygeupolia* in respect to the Eupoliidæ and the Lineidæ, it seems to belong entirely to neither, but to have affinities with both. It possesses the leading characteristic of the Eupoliidæ, but all the other attributes of that family are greatly modified. In general structure *Zygeupolia* comes nearest to the Micruran Lineidæ, although it is evident that it must be regarded as an aberrant member of that family.

But is *Zygeupolia* a retrograde member of the Lineidæ, or merely a more simple, primitive form in process of becoming more complex?

It is generally accepted that the Eupoliidæ are more primitive than the Lineidæ. Now *Zygeupolia*, in the absence of the lateral

slits, possesses a character that is general in the Eupoliidæ and exceptional in the Lineidæ; the number and arrangement of the muscular layers of the proboscis make a second character only occasional in the Lineidæ, and, finally, variations occur in the number of the proboscis crosses in *Zygeupolia*, a character that is constant in the Lineidæ. Therefore *Zygeupolia*, with one primitive character, a second corresponding to a reduced number of parts in the Lineidæ, and a third that varies in different individuals, is undoubtedly a form in transition from a more simple and primitive condition to a complex state. It may be regarded as the most primitive member of the Lineidæ yet described.¹⁸

In general external characters, *Zygeupolia* comes nearer to the genus *Micrura* than to any of the other genera of the Lineidæ. The generally small size, the body more or less rounded posteriorly and the presence of a caudicle are characters common to both. To *Micrura cvea*, *Zygeupolia* bears a most striking resemblance in size, shape and color, and the two can scarcely be distinguished except with a hand lens, which reveals the presence of lateral slits in the former and their absence in the latter.

The relation of the Heteronemerteans to the Protonemerteans is an interesting question. The position of the lateral nerve chords is relatively the same in both, the outer longitudinal muscle layer of the Heteronemerteans being merely a later formation from the ectoderm (Bürger, 1894), and the cutis glands being formed by the sinking beneath the surface of certain epithelial gland cells. Lateral slits are absent among the more simple Eupoliidæ, and I hope to have shown in this paper that an inner circular muscle layer, or its derivatives, is quite common among the Heteronemerteans.

It seems to me that the Heteronemerteans are very closely related to the Protonemerteans, the Lineidæ being connected by forms like *Zygeupolia*, the Eupoliidæ and *Hubrechtia*, and that the Metanemerteans and the Mesonemertean *Cephalothrix* are widely divergent forms.

¹⁸Since the above was written the new Heteronemertean, *Micrella rufa* Punnett (1901 *b*), has been described as the most primitive member of the Lineidæ. But *Zygeupolia*, in entering the family of the Lineidæ, must assume the lowest position until an even more primitive form is discovered. Within the last few years so many new Nemertean genera have been found that we may look confidently for further additions to the group.

In regard to *Carinoma*, I agree with the view recently advanced by Bergendal (1900 *b*) that it is more of a Protonemertean than a Mesonemertean, for its points of agreement with the Protonemerteans are far more numerous than with *Cephalothrix*. Bergendal's suggestion to retain Hubrecht's broader order of the Palæonemertini, including the four families of the Carinellidæ, Carinomidæ, Hubrechtidæ and Cephalothricidæ, seems a very excellent one. This suggestion is based upon a comparative study of *Carinoma* and upon the discovery of the interesting form *Callinera bürgeri*, a true Protonemertean, in which the cerebral organs are absent.

In all zoölogy, as our knowledge advances and more and more new forms are discovered, the gaps between old and once widely separated families and groups are gradually filled and the results tend toward a more elastic and broader classification.

The view is held by some zoölogists that the Nemerteans, on account of their general uniformity, are a comparatively recent group, so that a large number of the members are probably still in existence. If this is true, we may expect some day, when our present species are better known and all the intermediate forms have been added to them, to see our existing lines of classification laid aside, and in their place one broad comprehensive group.

LITERATURE.

[The papers not seen by the writer are marked with an asterisk.]

- 1900a. BERGENDAL, D. Ueber ein Paar sehr eigenthümliche nordische Nemertinen. *Zool. Anz.* Bd. 23, No. 617.
- 1900b. BERGENDAL, D. Bör ordningen *Palæonemertini* Hubrecht uppdelas i tvänne ordningar *Protonemertini* och *Mesonemertini*? *Kongl. Vetenskaps-Akad. Förhandlingar*, No. 6. Stockholm.
- 1900c. BERGENDAL, D. Till kännedom om de nordiska Nemertinerna. *Kongl. Vetenskaps-Akad. Förhandlingar*, No. 5. Stockholm.
- 1898. BÖHMIG, L. Beiträge zur Anatomie und Histologie der Nemertinerna (*Stichostemma græense* [Böhmig], *Geonemertes chalicophora* [Graff]). *Zeit. f. Wiss. Zool.* Bd. 64.
- 1890. BÜRGER, O. Untersuchungen über die Anatomie und Histologie der Nemertinen, nebst Beiträgen zur Systematik. *Zeit. f. Wiss. Zool.* Bd. 50.
- 1891. BÜRGER, O. Die Enden des excretorischen Apparates bei den Nemertinen. *Zeit. f. Wiss. Zool.* Bd. 53.
- 1892. BÜRGER, O. Was sind die Attractionsphären und ihre Centralkörper? *Anat. Anz.* Bd. 7.
- 1894. BÜRGER, O. Studien zu einer Revision der Entwicklungsgeschichte der Nemertinen. *Ber. d. Nat. Ges. Freiburg.* Bd. 8.
- 1895. BÜRGER, O. Die Nemertinen des Golfes von Neapel. *Flora u. Fauna des Golfes von Neapel.* XXII. Monographie.

- 1897-99. BÜRGER, O. Nemertini. *Bronn's Klassen u. Ordnungen*. Bd. IV, Suppl.
- *1851. BUSCH. Beobachtungen über Anatomie und Entwicklung einiger wirbellosen Seethiere. Berlin.
- 1895a. COE, W. R. On the Anatomy of a Species of Nemertean (*Cerebratulus lacteus* Verrill), with Remarks on certain other Species. *Trans. Connect. Acad.* Vol. 9.
- 1895b. COE, W. R. Description of Three New Species of New England Palæonemerteans. *Ibid.*
1901. COE, W. R. Papers from the Harriman Alaska Expedition. XX. The Nemerteans. *Proc. Washington Acad. Sci.* Vol. 3.
- *1853. DALYELL, J. G. The Powers of the Creator. London.
1851. DIESING, C. M. Systema Helminthum. Vol. 1. Vindobonæ.
- *1847. FREY, H., and R. LEUCKART. Beiträge zur Kenntniss wirbelloser Thiere. Braunschweig.
1882. v. GRAFF, L. Monographie der Turbellarien. 1. Rhabdocœlida. Leipzig.
1855. GRUBE, E. Bemerkungen über einige Helminthen und Meerwürmer. *Arch. f. Naturges.* Jahrg. 21.
1831. HEMPRICH et EHRENBURG. Symbolæ Physicæ. Animalia evertibrata exclusis Insecta percensuit Dr. C. G. Ehrenberg. Berolini.
1887. HUBRECHT, A. A. W. Report on the Nemertea collected by H. M. S. "Challenger" during the years 1873-1876. "Challenger" Report, Vol. 19.
1865. JOHNSTON, G. A Catalogue of the British Non-Parasitical Worms in the Collection of the British Museum.
1862. KEFERSTEIN, W. Untersuchungen über niedere Seethiere. *Zeit. f. Wiss. Zool.* Bd. 12.
1848. KÖLLIKER, A. Beiträge zur Kenntniss niederer Thiere. *Zeit. f. Wiss. Zool.* Bd. 1.
1858. KROHN, A. Ueber Pilidium und Actinotrocha. *Arch. f. Anat., Physiol. und wiss. Med.* Jahrg. 25.
1896. LEE, A. B. The Microtomist's Vade-Mecum. London, 4th ed.
1858. LEUCKART, R. Bericht über die Leistungen in der Naturgeschichte der Niederen Thiere während des Jahres 1858. *Arch. f. Naturges.* Jahrg. 25, Bd. 2.
1858. LEUCKART and PAGENSTECHER. Untersuchungen über niedere Seethiere. *Arch. f. Anat., Physiol. u. wiss. Med.* Jahrg. 25.
1869. METSCHNIKOFF, É. Studien über die Entwicklung der Echinodermen und Nemertinen. *Mém. de l'Acad. Imp. des Sci. de St. Pétersbourg*. VII^e Sér., T. 14.
1867. M'INTOSH, W. C. On the Gregariniform Parasite of Borlasia. *Trans. R. Micr. Soc. London*. Vol. 15.
1869. M'INTOSH, W. C. On the Structure of the British Nemerteans and some new British Annelids. *Trans. R. Soc. Edinburgh*. Vol. 25.
1874. M'INTOSH, W. C. A Monograph of the British Annelids. Pt. 1 continued. The Nemerteans. London. Ray Society.
1875. M'INTOSH, W. C. On Valencinia Armandi, a new Nemertean. *Trans. Linn. Soc. London* (2). Vol. 1.
1879. M'INTOSH, W. C. Marine Annelids from Kerguelen Land. *Phil. Trans. Roy. Soc. London*. Vol. 168.
1894. MONTGOMERY, T. H. Stichostemma eilhardi nov. gen., nov. spec. Ein Beitrag zur Kenntniss der Nemertinen. *Zeit. f. Wiss. Zool.* Bd. 59.
- 1897a. MONTGOMERY, T. H. On the Connective Tissue and Body Cavities of the Nemerteans, with Notes on Classification. *Spengel's Zool. Jahrb.* Vol. 10.

- 1897*b*. MONTGOMERY, T. H. Studies on the Elements of the Central Nervous System of the Heteronemertini. *Journ. Morph.* Vol. 13.
 1854. MÜLLER, J. Ueber verschiedene Formen von Seethieren. *Arch. f. Anat., Physiol. u. wiss. Med.* Jahrg. 21.
 1788. MÜLLER, O. F. *Zoologica Danica.* Havniæ.
 1855. OUDEMANS, A. C. The Circulatory and Nephridial Apparatus of the Nemertea. *Quart. Journ. Micr. Sci.* Vol. 25.
 1900. PUNNETT, R. C. On a Collection of Nemerteans from Singapore. *Quart. Journ. Micr. Sci.* Vol. 44.
 1901*a*. PUNNETT, R. C. Nemerteans. *Fauna and Geog. of Maldive and Laccadive Archipelagoes.* Vol. I, Pt. 1.
 1901*b*. PUNNETT, R. C. On Two New British Nemerteans. *Quart. Jour. Micr. Sci.* Vol. 44.
 1846. QUATREFAGES, A. de. Etudes sur les types inférieurs de l'embranchement des Annelés. *Ann. des. Sci. Nat.* (3) T. 6.
 1900*a*. THOMPSON, C. B. Preliminary Description of *Zygeupolia litoralis*, a new Genus and new Species of Heteronemertean. *Zool. Anz.* Bd. 23, No. 610.
 1900*b*. THOMPSON, C. B. *Carinoma tremaphoros*, a new Mesonemertean Species. *Zool. Anz.* Bd. 23, No. 631.
 1893. VERRILL, A. E. The Marine Nemerteans of New England and Adjacent Waters. *Trans. Connecticut Acad.* Vol. 8.
 1895. VERRILL, A. E. Supplement to the Marine Nemerteans and Planarians of New England. *Trans. Connecticut Acad.* Vol. 9.
 1863. WAGENER, G. R. Ueber die Muskelfaser der Evertebraten. *Arch. f. Anat., Physiol. u. wiss. Med.* Jahrg. 30.
 1896. WHEELER, W. M. The Sexual Phases of *Myzostoma*. *Mitt. aus der Zool. Stat. zu Neapel.* Bd. 12.
 1900. WILSON, C. B. The Habits and Early Development of *Cerebratulus lacteus* (Verrill). *Quart. Jour. Micr. Sci.* Vol. 43.

EXPLANATION OF PLATES XL-XLIV.

All figures, except fig. 63, refer to *Zygeupolia*. The outlines of all figures, except figs. 1, 4, 5, 6, have been drawn with the camera lucida of Zeiss.

The following reference letters are used in the figures :

A., anus.
 Abs. C., absorptive cell.
 b., swollen portion of testis duct.
 B. L., basement layer.
 B. M., basement membrane.
 Bl. M., muscle of blood vessels.
 B. W., body wall.
 b. k., basal knob.
 Bl. f. C., blood-forming cell.
 Bl. L., blood lacuna.
 C., candicle.
 C. W., candicle wall.
 C. L. N., candicle nerve.
 Cn. T., connective tissue.
 Cn. T. N., connective tissue nucleus.
 Cn. T. S., connective tissue sheath.
 Contr., contracted area.
 Chr., chromatin.
 Cil., cilia.
 Ctl., cuticle.

Cu. Gl.₁, red-staining cutis gland cell—coarse type.
 Cu. Gl.₁₁, red-staining cutis gland cell—fine type.
 Cu. Gl.₂, blue-staining cutis gland cell.
 Cy., cytoplasm.
 C. N., cerebral nerve.
 C. Org., cerebral organ.
 C. Org. V., cerebral organ blood vessel.
 C. M., circular muscle.
 C. M. p. s., circular muscle of proboscis sheath.
 Cil. C., ciliated canal.
 Cil. P., ciliated pit.
 D. Comm., dorsal commissure.
 D. L., dorsal lobe.
 D. N., dorsal nerve.
 D. V., dorsal blood vessel.

- D.m.cr.*, dorsal muscular cross.
Dl.V., dorso-lateral blood vessel.
dt., duct.
E.I., end intestine.
Ep., epithelium.
Ep.M., epithelial muscle.
Ep.p.s., epithelium of proboscis sheath.
Ep.m.f., epithelial muscle fibrils.
End., endothelium.
Exc.d., excretory duct.
G.C., ganglion cell.
G.C.i., ganglion cell I.
G.C.ii., ganglion cell II.
G.C.iii., ganglion cell III.
Gl.₁, red staining gland cell.
Gl.₂, blue-staining gland cell.
Gl.R., glandular ridge.
Gon., gonad.
Gon.W., gonad wall.
H.M., horizontal muscle.
H.V., head blood vessel.
i.C.M., inner circular muscle.
i.L.M., inner longitudinal muscle.
i.B.L., inner basement layer.
i.Ep., inner epithelium.
i.O.mb., inner egg membrane.
I.Cæ., intestinal cæcum.
L.G., lateral groove.
L.M., longitudinal muscle.
L.M.f., longitudinal muscle fibre.
L.M.p.s., longitudinal muscle of proboscis sheath.
L.N., lateral nerve.
L.V., lateral blood vessel.
l.D.N., lower dorsal nerve.
mes., mesenchym.
M., mouth.
m.b., middle piece.
M.V., median blood vessel.
M.I., middle intestine.
M.s., muscle strand.
N., nucleus.
N.₁, nucleus that has divided amitotically.
N.Par., nucleus of parasite.
n., nucleolus.
n.vac., nucleolar vacuole.
n.p., nerve plexus.
Nph., nephridia.
Nph.D., nephridial main duct.
Nph.d., nephridial ductule.
Oes., œsophagus.
Oe.N., œsophageal nerve.
Oe.N.Comm., œsophageal nerve commissure.
Oe.Ep., œsophageal epithelium.
Ov., ovary.
O., ovarian egg.
O.₁, youngest ovarian egg figured.
O.₂, slightly older than *O.₁*.
O.₃, slightly older than *O.₂*.
o.O.mb., outer egg membrane.
o.Ep., outer epithelium.
o.C.M., outer circular muscle.
o.B.L., outer basement layer.
P., proboscis.
P.N., proboscis nerve.
P.S., proboscis sheath.
P.p., proboscis pore.
Par., parasite.
Re., rhynchocœl.
Rd., rhynchodæum.
Rd.m., rhynchodæum muscle.
Re.Ep., rhynchocœl epithelium.
Rhb., rhablites.
r.m.f., radial muscle fibres.
S., stomach.
S.Ep., stomach epithelium.
S.C., supporting cell.
Sec., secretion.
st., stalk.
Spg., spermatogonia.
Spz., spermatozoa.
T., testis.
T.d., testis duct.
Th., secretions (?) of proboscis epithelial cells.
T.B., terminal bulb.
u.D.N., upper dorsal nerve.
u.k., upper knob.
V.Comm., ventral commissure.
V.L., ventral lobe.
V.bl.con., ventral blood connective.
V.m.cr., ventral muscular cross.
u., subepithelial œsophageal gland cells.
x., intracellular ciliary prolongations.
Xd., dorsal muscular cross of proboscis.
Xc., ventral muscular cross of proboscis.
y., attachment of proboscis to body wall.
yk., yolk.
z., bending out of fibres from inner part of proboscis sheath.

PLATE XL, Fig. 1.—Diagrammatic horizontal optical section of the anterior part of the body.

Fig. 2.—Combined drawing of parts of a cross section of the body epi-

thelium and the outer longitudinal muscle layer, from the brain region. Gilson's fluid. $\times 604$.

Fig. 3.—Ganglion cell IV (neurochord cell), from the ventral brain lobe. $\times 1120$.

Fig. 4.—Sketch of living worm, natural size and color. This represents the appearance of the worm in extension; the posterior end is thin and flattened and the colors are dull. The light colored median line represents the rhynchocoel.

Fig. 5.—Sketch of living worm, natural size. The worm is at rest, but not contracted, and the colors are brighter than in the extended state. The cross lines in the posterior part indicate the intestinal caeca and the gonads.

Fig. 6.—Sketch of living worm, natural size, at rest. The white spots in the posterior part represent parasites.

Fig. 7.—Supporting cell from the epithelium of the ciliated pit of the cerebral organ. $\times 1120$.

Fig. 8.—Ganglion cell III, from the brain. $\times 1120$.

Fig. 9.—Ganglion cell I, from the brain. $\times 1120$.

Fig. 10.—A cluster of ganglion cells of type II, from the ventral brain lobe. $\times 1120$.

Fig. 11.—Two gland cells from the epidermis of the caudicle, in an early phase of secretion. $\times 1120$.

Fig. 12.—Portion of a cross section of the caudicle epidermis. $\times 604$.

Fig. 13.—A part of the circular muscle layer from the posterior end of the body, in longitudinal section. Flemming's fluid, iron-haematoxylin. *Contr.* represents the contracted fibrillar areas which occur at regular intervals, with light non-contracted regions between. Smaller contracted streaks may be seen half-way between the larger ones. $\times 320$.

Fig. 14.—Two supporting cells from a cross section of the body epithelium. Flemming's fluid, saffronin, gentian violet and iodine. The stalks are relatively longer than in preparations from different fixatives. *x.* indicates the intracellular ciliary prolongations. $\times 2200$ circ.

Fig. 15.—Cells of the body epithelium and cutis gland cells, from posterior end of the body. The blue-staining cutis glands of this region are much shorter than the red-staining glands, and both are smaller than the similar glands of the anterior end. Gilson's fluid. $\times 604$.

Fig. 16.—Optical horizontal section of the brain and mouth region. The main outlines drawn from life and diagrammatized. The blood system (in red) and the oesophageal nerve commissure are reconstructed from sections. $\times 29$.

Fig. 17.—Optical horizontal section of the posterior end of the body and the caudicle. The main outlines drawn from life and diagrammatized. The blood system (in red) is reconstructed from sections. $\times 29$.

PLATE XLI, Fig. 18.—Part of a cross section through the head, anterior to the brain. The rhynchodæum, *Rd.*, surrounded by four bundles of longitudinal muscle, *Rd.m.*, occupies the centre of the section. From the interlacing of the radial muscle fibres, *r.m.f.*, a layer of circular muscle, *C.M.*, is formed, which becomes the circular muscle of the proboscis sheath. $\times 70$.

Fig. 19.—Part of a cross section of the brain through the dorsal commissure, showing that the dorsal commissure in this specimen is composed of fibres coming from both dorsal and ventral lobes. The attachment of the proboscis to the body wall is also shown. $\times 70$.

Fig. 20.—Part of a cross section of the body through the ventral brain commissure. The section is rather obliquely cut, so that the right and left sides are not quite similar. $\times 70$.

Fig. 21.—Part of a cross section of the body through the cerebral organs. The section is quite oblique, so that its plane passes through the anterior part of the cerebral organ and the ciliated pit, *Cil.P.*, but through the posterior end of the left cerebral organ. $\times 70$.

Fig. 22.—Part of a cross section of the body through the œsophageal region. The anterior end of the nephridial main duct, *Nph.D.*, is shown, and the large expanded ventral blood connectives, *V.bl.con.*, are very prominent. $\times 70$.

Fig. 23.—Part of a cross section of the body immediately in front of the beginning of the middle intestine, showing the inner circular muscle layer, *i.C.M.*, and the dorsal and ventral muscular crosses, *D.m.cr.*, *V.m.cr.*, between the inner and outer circular muscle layers. The much enlarged upper and lower dorsal nerves, *u.D.N.*, *l.D.N.*, are very prominent. $\times 70$.

Fig. 24.—Part of a cross section of the body of a male in the region of the gonads. The plane of the section passes through one of the intestinal caeca, *I.Cae.*, and the narrower part of the testis. The duct of the right hand testis is shown, *T.d.* The sexual products of this individual are only partly mature, most of the cells being in the spermatogenic stage, *Spg.* $\times 70$.

Fig. 25.—Part of a cross section of the body of a female in the region of the gonads. The oldest ova, *O.*, are free in the centre, the youngest are attached to the wall of the gonad. Two encysted parasitic bodies, *Par.*, are present in the left-hand ovary. $\times 70$.

Fig. 26.—Cross section through the posterior region of the body, showing the simple end intestine, *E.I.*, without lateral caeca, and the two dorso-lateral blood vessels, *Di.V.*, that have resulted from a forking of the dorsal vessel. The gonads are absent from this region. $\times 70$.

Fig. 27.—Cross section through the junction of the caudicle with the body; the upper part of the figure belongs to the body, the lower part to the caudicle. The different character of the walls of the two parts is very evident. The end intestine, *E.I.*, has a dorsal position, and is about to open into the anus.

Fig. 28.—Cross section through the caudicle, showing the caudicle wall and the central blood lacuna, *Bl.L.* The great numbers of connective tissue cells, *Cn.T.N.*, actually present are, for the sake of clearness, only approximately represented. $\times 320$.

PLATE XLII, Fig. 29.—Portion of a cross section of the epithelium of the median blood vessel. $\times 604$.

Fig. 30.—Part of a cross section of the proboscis sheath, about 1.8 mm. in front of the beginning of the middle intestine, showing the origin of the inner circular muscle layer from circular fibres of the proboscis sheath. The innermost circular fibres of the proboscis sheath bend outward at *z.* and run beneath the stomach, thus forming the inner circular muscle layer. $\times 240$.

Fig. 31.—Part of a cross section of the epithelium of the œsophagus, from the anterior region, showing the subepithelial gland cells, *w.* $\times 604$.

Fig. 32.—Portion of the epithelium of the stomach, from a cross section. $\times 604$.

Fig. 33.—Half of a cross section of the alimentary tract through the junction of the œsophagus and the stomach. The upper part of the figure shows the epithelium of the stomach, *S.Ep.*; the lower part that of the œsophagus, *Oe.Ep.* A fold, *f.*, probably represents a primitive valve. $\times 320$.

Fig. 34.—Part of a cross section of the epithelium of the middle intestine from the posterior region. The cilia are slightly diagrammatic, being usually massed together in fixed preparations. $\times 604$.

Fig. 35.—Cross section through the "anterior region" of the proboscis. $\times 320$.

Fig. 36.—Cross section through a portion of the "glandular ridge" of the proboscis, showing several aggregations of rhabdites, *Rhb.* $\times 604$.

Fig. 37.—Tangential section of a portion of the proboscis from the "mid-

dle region," showing the longitudinal muscle, *L.M.*, with the subepithelial muscle fibrils above, running transversely. $\times 604$.

Fig. 38.—Part of a longitudinal section of the proboscis, from the "middle region," showing the subepithelial muscle fibrils in transverse section. The outer flattened epithelium is extremely thin. $\times 1120$.

Fig. 39.—Part of a longitudinal section of the proboscis, from the "posterior region." The outer epithelium, *o.Ep.*, is composed of cells of considerable height, with abundant cytoplasm. The subepithelial muscle fibres, *Ep.m.f.*, are thickened in this region. $\times 1120$.

Fig. 40.—Cross section through the "middle region" of the proboscis, showing both dorsal and ventral muscular crosses, *Ad.*, *Xc.* The lateral nerves form a continuous plexus, *n.p.* The glandular ridge of the dorsal surface is very prominent, *Gl.R.* $\times 320$.

Fig. 41.—Cross section through the "posterior region" of the proboscis, some distance anterior to its termination. The proboscis nerves are again separate, *P.N.* $\times 320$.

Fig. 42.—Small "rhynchocœl corpuscles." $\times 1120$.

Fig. 43.—Large cells from the fluid of the rhynchocœl, "rhynchocœl corpuscles." The two nuclei, *N.*, are probably the result of amitosis. $\times 1120$.

Fig. 44.—Portion of a cross section of the proboscis immediately posterior to its insertion, showing the regular brick-shaped cells of the outer epithelium, *o.Ep.* The subepithelial muscle fibrils are absent from this, the most anterior, region. $\times 604$.

PLATE XLIII, Fig. 45.—Portion of a cross section through the body wall, showing the excretory duct of the left nephridium, *Ecc.d.* $\times 128$.

Fig. 46.—Portion of a cross section of the body, showing the left lateral blood vessel, *L.V.*, with the adjacent nephridial main duct, *Nph.D.*, and a ductule, *Nph.d.* $\times 320$.

Fig. 47.—Portion of a cross section of the body, showing the right lateral blood vessel, *L.V.*, into which project two terminal bulbs of the nephridia, *T.B.* The epithelium of the blood vessel is not continued around the ends of the terminal bulbs. $\times 604$.

Fig. 48.—Cross section of an ovum infected with a stage of a parasite older (?) than that shown in fig. 61. $\times 604$.

Fig. 49.—Cross section of one of the dorso-lateral blood vessels. $\times 604$.

Fig. 50.—Portion of a cross section through the anterior part of the rhynchocœl, showing the dorsal blood vessel. The endothelium, *End.*, of the ventral wall of the vessel is very distinct, but that of the dorsal wall is interrupted by the proliferation of blood-forming cells, *Bl.f.C.* $\times 604$.

Fig. 51.—Cross section of the dorsal blood vessel after it has left the rhynchocœl. A network of connective tissue cells, *Cn.T.N.*, surrounds the blood vessel. $\times 604$.

Fig. 52.—Cross section of the oldest stage of an immature ovum, free in the centre of the gonad. The thick outer, *o.O.mb.*, and the thin inner, *i.O.mb.*, egg membranes are shown. $\times 604$.

Fig. 53.—Surface view of the gonad epithelium. $\times 604$.

Fig. 54.—Portion of a cross section through an ovary, containing only young stages. *O.*₁ represent the youngest ova figured, *O.*₂ and *O.*₃ older forms. $\times 240$.

Fig. 55.—Portion of a cross section of the body wall, showing a testis duct, *T.d.*, with an expanded distal portion, *b.* The longitudinal muscle layers of the body wall are not indicated. $\times 320$.

Fig. 56.—Horizontal optical section of a portion of the posterior body region. Drawn from life, showing gonads filled with ova between the intestinal cæca. The large body, *Par.*, in the middle gonad is the cyst of a parasite. $\times 70$.

Fig. 57.—Portion of a cross section through the testis, showing the marginal spermatogonia. $\times 604$.

Fig. 58.—Spermatozoa, the middle piece seen in side view and appearing bilobed. A minute point is present at the tip of the head. Iron-haematoxylin, strongly destained. $\times 1120$.

Fig. 59.—Spermatozoan, and a detached middle piece, *m.b.*, which is four-lobed. Iron-haematoxylin, not strongly destained. $\times 1120$.

Fig. 60.—Portion of a cross section through the body wall and ovary, showing an encysted stage of a parasite, *Par.* The striated cuticle, *Ctl.*, is surrounded by a delicate membrane. Two egg nuclei, *N.*, are to be seen in the cytoplasm at the base of the cyst.¹⁹ The nucleus within the cyst, *N.Par.*, is amoeboid. $\times 320$.

Fig. 61.—Cross section of an ovum infected with a young (?) stage of a parasite, *Par.* $\times 604$.

PLATE XLIV, Fig. 62.—Part of a cross section of the body wall through one of the "lateral grooves," *L.G.* The individual cells of the groove are not clearly distinguishable with this magnification. 95 per cent. alcohol. $\times 320$.

Fig. 63.—Portion of a cross section through the body wall of *Parapollia aurantiaca* Coe, showing the "lateral groove." The "lateral groove" is here everted, and appears as an elevation above the general surface level. The cutis glands, *Cu.Gl.*₂ of the "groove" are large and are not found in other parts of the section. $\times 40$.

¹⁹The reference line from *Ctl.* only extends as far as the egg membrane, instead of to the cuticle within.